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KØBENHAVN
C. A. REITZELS FORLAG
BIANCO LUNOS BOGTRYKKERI A/S
1944

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EXPERIMENTS ON MERISTIC AND OTHER CHARACTERS IN FISHES

I. ON THE INFLUENCE OF TEMPERATURE ON SOME MERISTIC CHARACTERS IN SEA-TROUT AND THE FIXATION-PERIOD OF THESE CHARACTERS

BY

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KØBENHAVN
C. A. REITZELS FORLAG
BIANCO LUNOS BOGTRYKKERI A/S
1944

CONTENTS

Page

Introduction ... 3

I. Experimental Equipment ... 5

II. Determination of the Age of the developmental Stages at different Temperatures (Day-Degrees) ... 7

III. Brief Survey of the environmental Conditions during the Experiments carried out in 1942—43 ... 7

1. Mortality during the Experiments ... 9
2. Temperature ... 9
3. Oxygen, Hydrogen Ion Concentration etc. ... 10

IV. Treatment of the preserved Material ... 12

V. Experiments concerning the Influence of Temperature ... 14

A. The Influence of high and low Temperatures on the average Number of Vertebrae and Fin-Rays of Sea-Trout 14

1. The Number of Vertebrae ... 14
2. The Number of Rays in the dorsal, anal and pectoral Fins ... 17

B. The Fixation-Period of some meristic Characters in Sea-Trout ... 19

1. The Vertebrae ... 19
2. The Rays in the dorsal, anal and pectoral Fins ... 28

VI. Abnormalities in the vertebral Column and the Significance of these Formations ... 32

VII. The experimental Results compared with certain so-called racial Differences in some marine Fishes ... 40

VIII. Survey and concluding Remarks ... 44

IX. Bibliography ... 49

X. Tables ... 52

Dansk Resumé ... 58

INTRODUCTION

Investigations into the meristic characters of fishes carried out with a view to describing races, particularly among the economically important species, have played a very prominent rôle within scientific fishery researches since HEINCKE's work on the herring races, published in 1898; during the last thirty to forty years much endeavour and much money has been spent on such investigations, in the hope of obtaining, *inter alia*, a wider and better knowledge of the localisation, the migrations etc. of the various stocks of fishes. Such research has indeed produced much material concerning the natural history of many species of fishes, but in view of the great sums annually spent upon it, it is apparently a singular fact, that no serious endeavours since those of JOHS. SCHMIDT have been made to obtain experimentally a more accurate knowledge of the variation of meristic characters and their development in relation to environment. However, the primary cause of this is evidently due to the fact, that up to now it has been impossible to experiment with salt water fishes, because artificial rearing of the tiny fry had so far been without any result. After GUNNAR ROLLEFSEN's successful experiments carried out for this purpose, using nauplii of *Artemia salina* as food, a new epoch within this field of fishery investigations may be expected, when the world has returned to its normal state.

Very little has been published about experiments carried out hitherto with the object of investigating the influence of the environmental factors on meristic characters in fishes. Here is a summary of the few experiments known to me.

Author	Year	Species	Character	Environmental factor
JOHS. SCHMIDT	1917	Lebistes reticulatus	Dorsal fin	t°
—	1919			
—	1920	Zoarces viviparus	Vertebrae	? ($S\ ^0/_{00}$, t°)
—	1921	Salmo trutta	Vertebrae	t°
MOTTLEY	1931	Salmo kamloops	Scales	t°
—	1934			
—	1937	Salmo gairdnerii kamloops	Vertebrae	t°
		— — whitehousei		O_2 ?
ROLLEFSEN	1940[1])	Pleuronectes platessa ♀	Vertebrae	t°
		× Pleuronectes flesus ♂	and fin rays	

With regard, however, to growth in fishes several experiments with fresh water fishes have been carried out, environmental factors like temperature, the space factor, flow of water

[1]) P. 216, no details given; see this paper p. 21.

etc. being varied (e. g. Hofbauer 1902 (*Cyprinus carpio*), Hall 1925 (*Coregonus clupeaformis*), Willer & Schnigenberg 1927 (*Salmo trutta fario*), Gray 1929 (*Salmo trutta fario*)). I may also refer to Knut Dahl's investigations (1943, new edition) into the importance of the size of the eggs for the subsequent growth of the fry of Trout and the problems connected with this phenomenon.

The establishment in 1938 of a special scientific department in „Danmarks Akvarium" closely connected with the laboratories of „Kommissionen for Danmarks Fiskeri- og Havundersøgelser" at Charlottenlund Slot, made it possible to start various experimental investigations, though under difficult conditions, owing to the outbreak of the war. As soon as the department had been opened in the autumn of 1940 I commenced, however, a series of experiments in order to study more closely the relation between environmental factors and for instance the meristic characters in fishes. I considered the Sea-trout (*Salmo trutta trutta* L.) to be best fitted for preliminary experiments, since we possess much experience regarding this species. This experience is derived partly from commercial hatcheries, partly from the late Professor Johs. Schmidt's experiments at the Carlsberg Laboratory, where for instance much knowledge regarding the construction of a suitable hatching apparatus for experiments with Trout has been gained through his well known studies, commenced in 1918 and continued during a series of years.

During the first couple of years the experiments gave but few results, because at first the several installations suffered various mishaps and took long to operate satisfactorily, and then because the spells of hard frost in 1940—42 caused the conduit-pipes to burst and were responsible for other break-downs. However, since the autumn of 1942 I have obtained some results which I trust may be of interest to biologists working on the meristic characters in fishes in applied fishery biology as well as in more theoretical science. In the following pages I shall mention some of the results so far obtained, pointing out, however, that these results ought to be regarded as of a preliminary nature only. In the present circumstances I consider it most convenient also to publish some results from investigations which have not yet received detailed and adequate attention; at present I do not know, however, if there will be any possibility of returning to them; and though they accordingly are not of a final character, I hope nevertheless that they may be of some value to experimenters starting on similar research.

The present investigation depends on many different links working exactly together; the complicated machinery with thermo-regulators, pumps, cooling installations etc. of a modern aquarium must be able to work unceasingly and accurately hour by hour, day by day, month by month; much care by day and by night is therefore required on the part of those engaged in this work; many analyses of the various environmental factors, and thousands of countings and calculations have to be carried out exactly to the best of human ability, and I must therefore call attention here to the share of my collaborators in the results of the investigation, thanking each of them by name:

Magister E. Bertelsen, Dr. phil. A. Bruun, Miss Esther Hansen, Mr. Gunnar Hansen, Magister F. Hermann, Mr. B. Jepsen, Mr. Th. Lindboe, Mrs. Inger Rosenberg and Magister F. Sogaard Andersen.

Moreover I wish to thank Mr. H. Holm Hansen, Lellinge Fiskeri, for his readiness to provide me always with the best obtainable specimens of Trout and in spite of all difficulties to have the fish delivered in good condition.

Particularly I wish to thank the Carlsberg Foundation for the grants to experimental work in the aquarium without which it would have been quite impossible to carry out the present and other investigations.

I. Experimental Equipment.

In order to keep a constant or comparatively constant temperature during the incubation of the eggs of Trout and other fishes, two practically uniform hatching apparatus were constructed for fresh water and salt water respectively; the first only is briefly described here, since none but experiments on eggs of Trout are treated in this paper. During the years 1940—43 the apparatus has been somewhat altered because my experiments proved this to be necessary. I shall here briefly describe only the method of the experiments carried out during 1942—43.

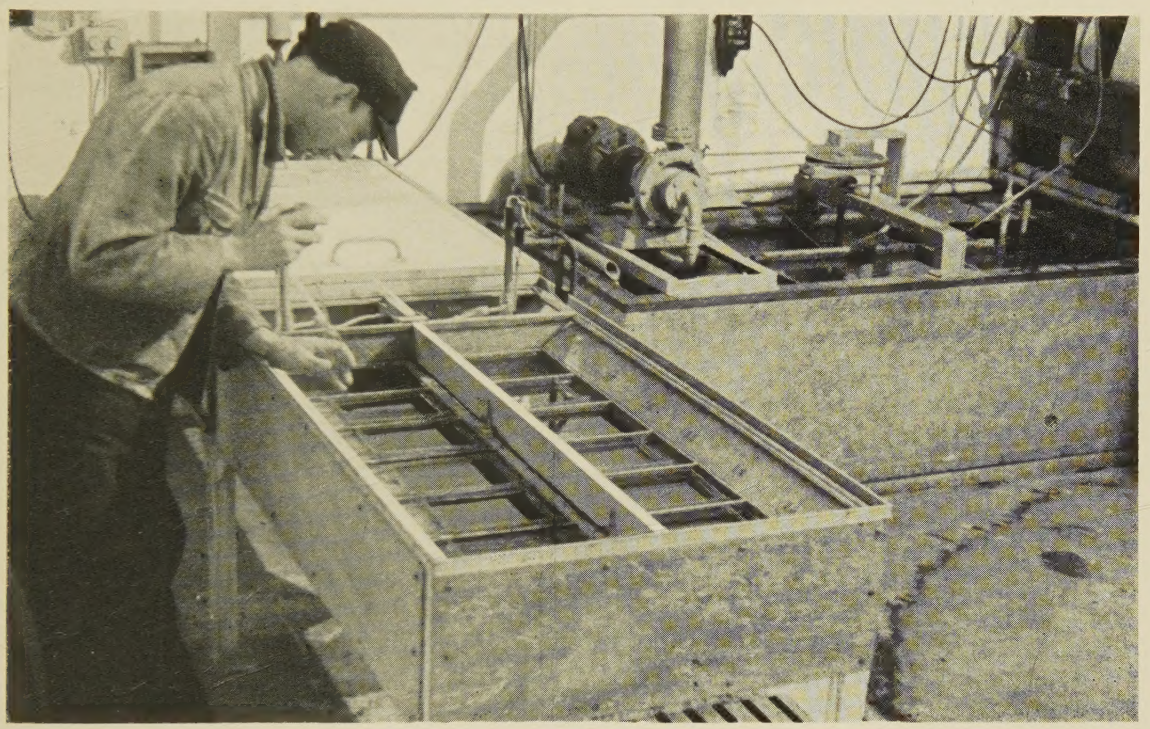

Fig. 1. The hatching apparatus. In the background to the right the cold water basin with pump etc. See the text.

Figs. 1 and 2 show the construction and size of the hatching apparatus. It is made of eternit and cement; the insulation consists of cork plates and insulated lids cover the rows of chambers in which the hatching boxes are placed. There is a total of 28 chambers distributed in four series, each with two inlet waterpipes, with water of a temperature of about 15° and 2.5° C. respectively (see the diagram fig. 2a); a temperature somewhat below that desired is obtained by regulating the water flowing through the inlet pipes. In the first chamber of each of the series the water is mixed, and a more accurate regulation of the temperature takes place here by means of a thermo-regulator and an electric heater. The water from the mixing chamber flows continuously through the following six chambers of the series in question and leaves the last chamber through an outlet pipe to return partly to the cold-water basin mentioned below, partly to the great fresh-water reservoir of the public aquarium.

Each of the six chambers contains a hatching-box made of celluloid, and, as in many hatcheries for Trout, the water is forced to flow through the chambers of each series through the perforated bottom of the celluloid box and out at the top through perforations in the back

wall of the box; fig. 2b shows a hatching-chamber with the hatching-box seen from above, and fig. 2c shows a section of a chamber with hatching-box; the arrows denote the course taken by the water through a hatching-chamber.

The warm water is led to the hatching apparatus from the great reservoir of the public aquarium; this water is aerated and is subjected to a thorough filtration through coal filters etc.

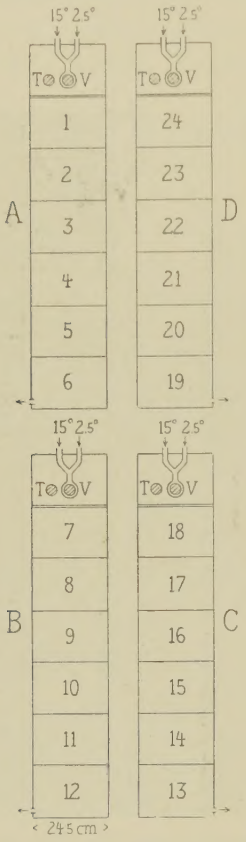

Fig. 2 a.

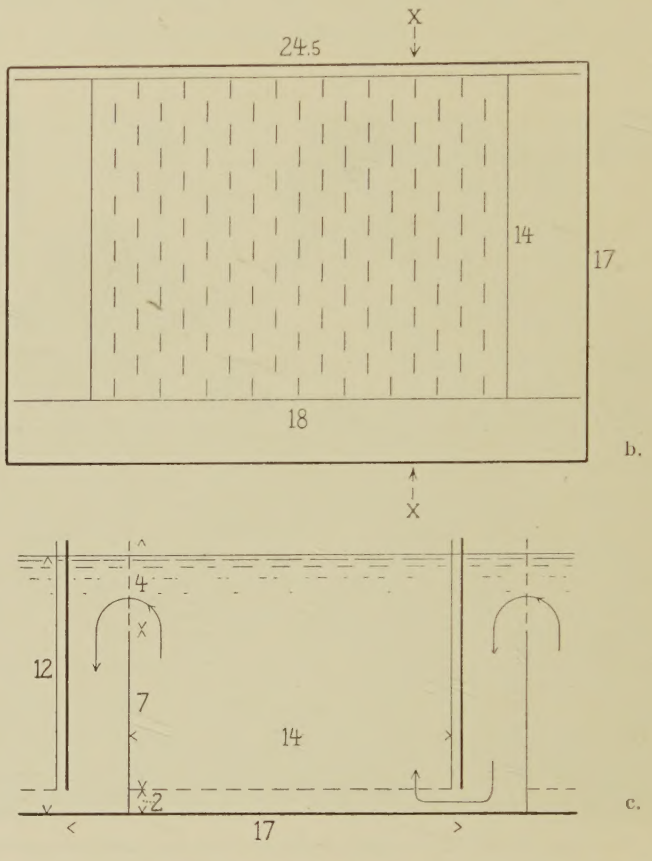

Fig. 2 b and c.

Fig. 2 a. Diagram of the hatching apparatus seen from above with its four series A, B, C, D. Measurements in cms. T = thermo-regulator; V = electric heater.

Fig. 2 b and c. Diagram of hatching chamber with hatching box seen from above, and (below) transverse section of the same showing the proportions. The arrows denote the course taken by the water. Measurements in cms. See moreover the text.

before it is led into the apparatus. The cold water is pumped into the apparatus from a special cold-water basin, the water of which is cooled down to about 2° by means of a cooling installation; the water from the cold-water basin is also filtered through a coal filter etc. before being led into the apparatus.

The water flows rather quickly through the hatching apparatus and is replaced 1—$2^1/_2$ times in the course of an hour. Infection of the eggs by fungi (e. g. Saprolegnia) or the like has not occurred during any of the experiments. A thin film of bacteria, however, appears on the surface of the water, but does not seem to be of any importance, since the water flows

undisturbed beneath; moreover the film is daily removed. As will be seen below, the hatching results prove that the conditions for the development of the eggs were very favourable.

Let me add that an alarm signal is set going if some important link in the arrangement fails and there is any too great change in temperature.

II. Determination of the Age of the developmental Stages at different Temperatures (Day-Degrees).

In some of the experiments mentioned below, it was of fundamental importance to transfer eggs in different stages of development from one temperature to another. In order to fix the date of the transfer I have used the number of day-degrees (D°)[1]), calculated from the hour of artificial fertilisation. As extreme temperatures — under 3° and above 9°[2]) — were not used in the experiments no objections can apparently be raised against using day-degrees (with 0° C. as zero) as a criterion for the transfers. At any rate this has proved most practical, since the use of one or more morphological characters during the course of development, e. g. the number of mesoderm segments or the like, meets with various difficulties. A comparison of the course of development in the numerous samples has shown that the stages of development at different temperatures varying between 3° and 9°, but at the same number of day-degrees, nearly correspond, or at any rate correspond so well that it is sufficient for the present studies. The stage of development reached during a certain number of day-degrees at the lower temperatures is, however, somewhat more advanced than at the higher temperatures; but the difference is not so great that it cannot be disregarded.

As the temperatures in the series were of course not exactly e. g. 3.0°, 6.0° or 9.0° the numbers of day-degrees are calculated in accordance with the actual daily average temperature in the mixing chamber of each series; the difference between these actual and the theoretical numbers of day-degrees was, however, quite insignificant (about 1 %).

In order to show the reader the relation of some of the stages of development to the number of day-degrees I have given in fig. 3, p. 8, some rough sketches of five embryos previous to hatching and also a newly hatched larva.

III. Brief Survey of the environmental Conditions during the Experiments carried out in 1942—43.

To give an illustration of the questions concerning the influence of the temperature on certain meristic characters, which I shall endeavour to elucidate in the present paper, I have preferred to use the results from one pair of Sea-trout, H × G. And in what follows I shall dwell on the conditions that prevailed during the incubation and rearing of the offspring of this pair; the offspring of another pair was incubated the same winter under quite the same conditions

[1]) Cf. papers by J. Reibisch (1902), A. C. Johansen and A. Krogh (1914). We use here 0° C. as biological zero even though it is scarcely quite correct.

[2]) Eggs of Trout (*Salmo trutta*) may develop at temperatures down to 0°, and at higher temperatures development may take place up to a temperature of 14°—17° C., but at these high temperatures mortality is great.

as that of H × G, and later on I shall return to various facts concerning this pair (E × F). Moreover, certain results from experiments carried out during other years shall be referred to and made use of.

The series of experiments was commenced December 17th 1942 with eggs of a female "H", fertilised artificially with sperm from a male "G". The experiment was kept going for about ten months, the last samples not being ready for preservation until September 10th 1943.

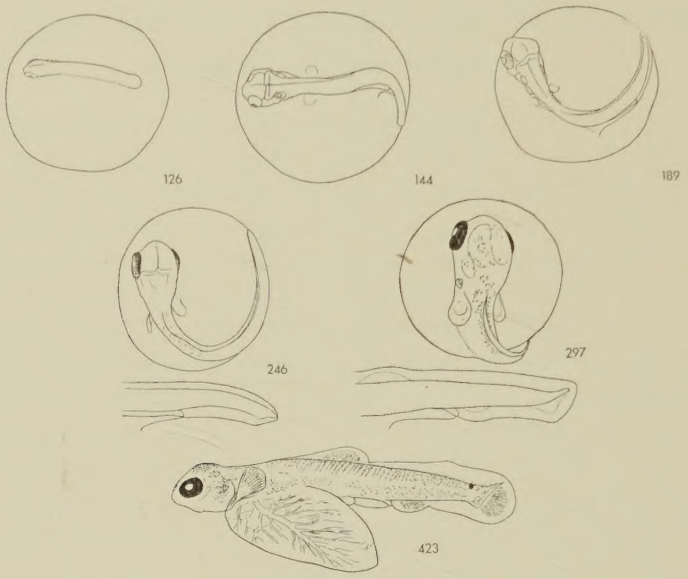

Fig. 3. Sketches showing a few developmental stages of Sea-trout in relation to the number of day-degrees. The egg membranes are removed in the five top figures representing unhatched embryos. Uppermost series: stages until the first traces of pigmentation in the eyes begin to show; intermediate series: "eyed-egg" stages; below: newly hatched fry. (Sketch by E. Bertelsen).

The female was a wild Trout just arrived from Lellinge near Køge Bugt, while the male had been kept in the public aquarium from 1941 and had reached the ripe stage there. While females could not be brought to the ripe stage in the aquarium, this male proved a success and has been used in the experiments during some years and is now in 1944 a strong specimen, 72 cms long. The female had 57 vertebrae, the number of vertebrae of the male is still unknown.

Immediately after fertilisation the eggs were placed in the hatching-boxes of the four series, of which one was kept at about 3° (A), one about 9° (C) and two series about 6° (B and D). The arrangement of the experiment is shown in the sketch fig. 2 p. 6. The hatching-boxes which as said are made of celluloid can easily be transferred from one hatching-chamber of a series to another without the eggs being disturbed by shaking or the like. The temperatures mentioned were used because I wished to operate with such ordinary temperatures as wild Trout might find in nature, without too great differences and with neither extremely high nor low temperatures.

We shall consider particularly the mortality and the temperature conditions during the experiments. Also various analyses of the water carried out during the experimental period shall be mentioned, primarily the content of oxygen and pH.

To begin with we shall observe, that the renewal of the water as mentioned has been fairly satisfactory, the entire amount of water in the hatching apparatus being renewed $1—2^1/_2$ times every hour.

At least once during 24 hours inspection of eggs and fry has been made, and dead eggs and fry have been removed; the hatching box has been cleaned by means of a siphon, if burst eggs, egg-shells and so forth on the bottom have made it necessary. During these operations electric light was used, while otherwise light has been excluded.

1. Mortality during the Experiments. This was less in the experimental series H × G than in any other experiment in which we have used Trout-eggs.

In the experimental series a total of 7.373 eggs from the female H were used. From the moment the fertilisation took place and until the hatching was finished, only 30 eggs died in all, i. e. only 0.4 % . This may be said to be a very fine result, and shows that the combination of the two specimens used as well as the conditions from fertilisation until hatching were unusual favourable. In one third of the 16 samples, each containing between 263 and 764 eggs, no egg died at all; most eggs died in the control sample at the higher temperatures, but 10 only out of a total of 764 eggs.

The mortality among the fry was a little greater particularly towards the time when the yolk was absorbed and preservation in formalin took place at about 800 D°; and of course several died in the experiments in which we examined the length of time during which it was possible to keep the fry alive without food (at the temperatures used, this limit seems to lie between 900 and 1000 D°). Experience about this was of some interest for the work, because I wished to see if the staining became better and the countings therefore more reliable, if the ossification was somewhat more advanced than at 800 D°. Considering now only the normal experiments which were concluded at about 800 D°[1]) and which are used in this investigation, the mortality among the hatched fry was only 2.4 % (112 out of 4654 hatched specimens).

From this it will be seen, that the mortality among eggs and fry have in no way had any influence on the results of the vertebrae-countings, which might have been the case if the mortality was particularly great, e. g. among the specimens with the highest number of vertebrae; selection of special variates therefore has been excluded.

2. Temperature. During the whole incubation period and the development, viz. from the fertilisation took place till the fry was preserved, endeavours were made to keep the temperature constant within each of the four series. In the case of the samples which were developed at the lowest temperature (3°), the fluctuations of temperature had to be watched closely from December 17th till September 10th, when the last sample was preserved. Owing, *inter alia*, to the fact that the series H × G promised well, the mortality being enormously low and excluding therefore any possibility of preference of certain variates during the development, it was my intention to select the results of these experiments as a basis for further experimental work; it was therefore of importance that the environment should be kept as constant as possible during the development, until the samples were preserved and used for counting of vertebrae, fin rays etc. The temperature was read two or more times in the course of the day; and if irregularities were found it was read many times during the day. Regulation of valves etc. was made at once, when greater fluctuations of the temperature were observed.

[1]) for a single sample, however, 903 D°.

Some accidents may of course be expected during so long an experimental period. The accidents occurred, however, only a few times and were due to failing of the relays, rupture of a thermo-valve and formation of ice in a valve of the cooling installation. Fluctuation of the temperature in the hatching boxes which these accidents might involve lasted, however, for a short time only, in most cases some few hours; only once did it last for 24 hours before repairs were finished and the machinery worked normally again. While the fluctuation of the temperature in the course of 24 hours very rarely reached 0.3°, the more serious accidents would cause a momentary rise up to 1°, and in some cases, though not in all the series, a rise up to about 2°. Unfortunately nearly all of the few accidents occurred within the first two months, while later on, previous to the hatching, there was no rise of any importance of the temperature. The most serious accident occurred only 12—13 days after fertilisation (this may be seen in fig. 4) but seems, however, without importance with regard to the results. As we now, since the accomplishment of the experiments, know that the influence upon the number of vertebrae makes itself felt during the period previous to 200 D°, the accidents mentioned were of course very unfortunate; but the results of the countings show on the other hand, that such insignificant fluctuations of short duration in the temperature do not seem to have any special influence upon the number of vertebrae. Now, however, this is going to be more closely examined, as we cannot so far absolutely assert that the fixing period may be of so short a duration that a rise or fall of the temperature within a few hours may not cause the maximum change of the number of vertebrae in the embryo.

In order to show the fluctuations in the average temperature during 24 hours we give in fig. 4 the temperature curves for the four series from the day of fertilisation until the development has advanced more than 3 months (corresponding to 300—900 D°). It will be seen from the figure that a serious rise or fall of the temperature has taken place only a few times within the period in which an influence on the characters examined particularly makes itself felt.

Among environmental factors with a supposed influence upon the number of vertebrae, the specific gravity of the water has also been mentioned. The specific gravity of the fresh water depends first of all on the temperature, and with the experimental arrangement which has been used it has therefore not been possible to investigate whether this factor as Johnsen (1936) supposes is of any influence.

3. Oxygen, Hydrogen Ion Concentration etc. In the commercial hatching of Trout, the amount of oxygen is considered adequate according to Buschkiel (1931, p. 238) when there is at least 6 cm^3 oxygen per litre, mediocre when there is 5 –6 cm^3, but still less amounts of oxygen may be tolerated. In the present experiment the amount of oxygen has nearly always when measured been over 6.5 cm^3, which at the prevailing temperatures gives a saturation percentage of oxygen between 70.7 and 92.0; the minimum amounts were observed but a few times, and always only at the outlet of the series with the higher temperatures (9° and 6°). The decrease or increase of oxygen from the first chamber to the last in the various series must presumably be considered as having no importance; the loss (at the higher temperatures) has usually been below 0.5 cm^3 per litre, though sometimes a little higher (0.6—0.8); and only once a loss of over 1 cm^3 has been observed (1.35 cm^3, 15.4 %, in the series B, March 10th ɔ: after the control sample in this series was hatched out). In the 3°-series loss of oxygen was not measured, but there was sometimes a slight increase.

Johansen and Krogh (1914 p. 31—32) state that an oxygen percentage of 50 is sufficient for the normal development of eggs and fry of the subject they used (the Plaice); and

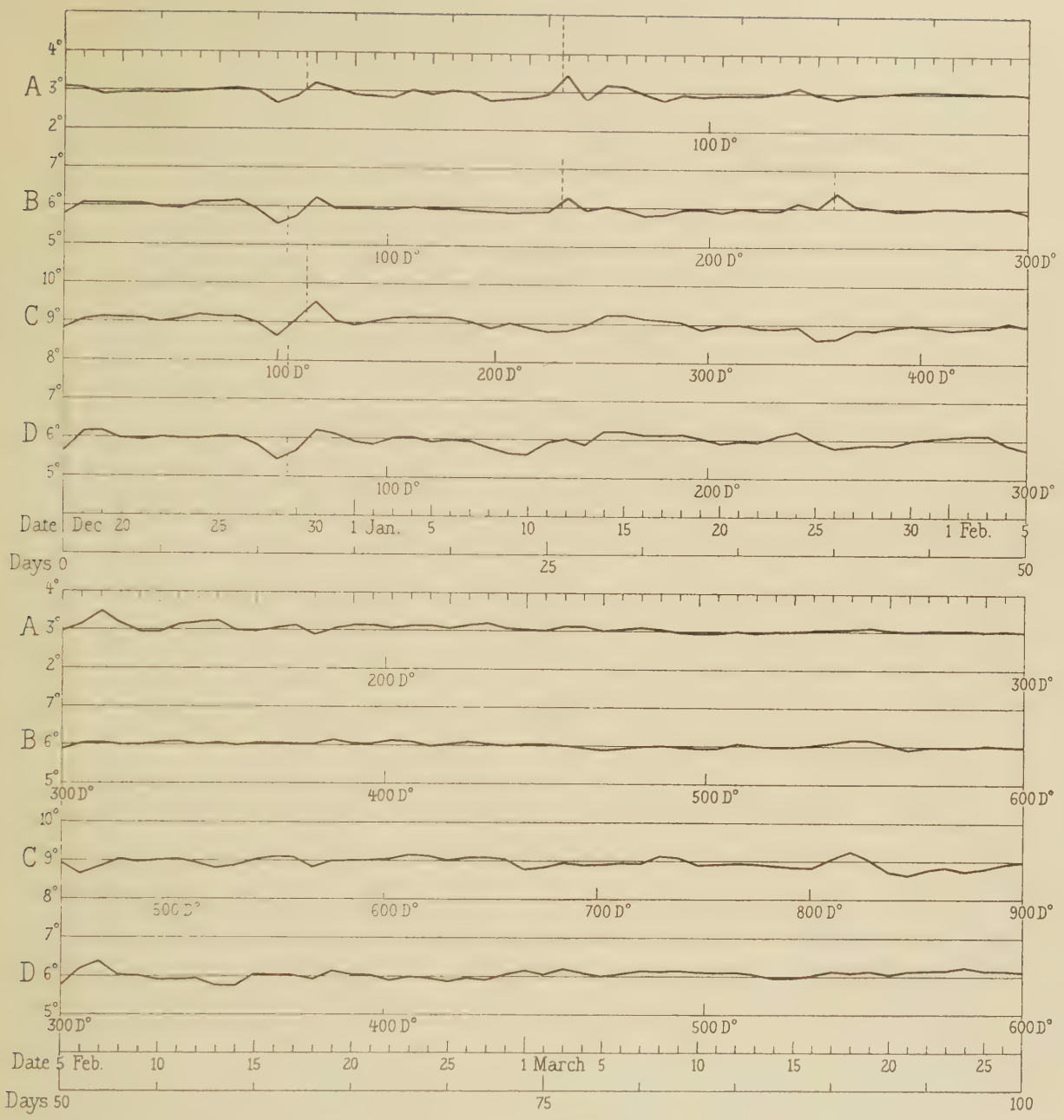

Fig. 4. Curves showing the daily average temperature during the first 100 days. Vertical dotted lines representing the maximum deviations of temperatures of 1° or more. A, B, C and D: the four series. Date, number of days, and of day-degrees (D°) indicated.

I suppose that the amount of oxygen in my experiments has been so great, that an influence producing another average number of vertebrae for that reason probably can be excluded. As the conditions in all four series have been fairly uniform with regard to the amount of oxygen (rarely inferior to 80 % oxygen), a displacement in the number of vertebrae must at any rate

have been somewhat the same in all series. Whether changes of the amount of oxygen in the water have any influence on the average number of vertebrae is, however, not yet proved experimentally.

I need not consider all the several other possible active factors, but will merely mention that endeavours were made all the time to keep the conditions in the various series of the aquarium quite uniform; thus pH has been very alike in all the series, as it has always been above 8, most often about 8.2—8.3.

It must further be mentioned, that the amount of salt in the water was almost the same in all four experimental series (S $^0/_{00}$ hardly over 0.1, most often much lower), and it must also be assumed, that other substances contained in the water (calcium, iron etc.) will have been practically the same in all the four series, as the water in all of them was of the same origin. The nitrate and phosphate content was measured occasionally and was for nitrate about 2500 mg.N/m^3, for phosphate about 150—180 mg.P/m^3. Experiments have been started in order to investigate, whether such considerable amounts of nitrate and phosphate are of any influence.

In some of the experiments a few of the samples had but half a chamber; this was, however, only the case for 6 samples, and all of these were in the eyed-eggs stage or hatched-out fry when transferred from a whole chamber to a half-sized one; and as all the samples which thus had different conditions as to space, but otherwise were treated like the others, show average numbers of vertebrae, which correspond almost exactly with those of the samples in the neighbouring chambers, it is impossible that conditions of space were of any influence with regard to the number of vertebrae; this is also quite improbable, as it is now known that the fixing of the number of vertebrae takes place previous to the eyed-eggs stage; and there moreover has been ample space in the various chambers (1—3 eggs per cm^2, though about 4 eggs could find room in one layer per cm^2).

Willer (1928) states, that light has influence on the speed of development; too much light delays the time of hatching. In my experiments the development of the eggs has taken place practically in darkness; the eggs being exposed to light only during the short interval when dead eggs were removed etc. Consequently this environmental factor too is apparently without any importance in the present experiments, all the eggs having been treated alike as to this factor; still we cannot exclude the possibility, that inspection by light might in certain cases expose a sample to the light at a moment when it is particularly liable to influence, and that thereby some influence that we cannot account for was induced.

We cannot of course quite exclude the possibility, that certain factors, which we have not observed or which we have considered without any importance may have had some influence.

I expect, however, that after all, the present experiments were carried out very nearly in accordance with what might be demanded in the case of experiments of this nature: only one single external factor, the temperature, has varied significantly from one series to another.

IV. Treatment of the preserved Material.

The fry is generally preserved when it is about 800 D° old, then the vertebrae and the fin-rays are clearly and distinctly developed, and the content of the yolk-sac almost absorbed. Need for food sets in some time before. If lack of food does not cause mortality to a greater extent about this time or a little later, the fry may, if no special need sets in, with advantage be

kept alive a little longer, e. g. up to 900 D°. In certain of the fundamental experiments (e. g. with H × G) I have, however, preserved practically all the fry at about 800 D°, hereby obtaining a uniform treatment of the material. If for instance feeding had taken place in the later stages of the development, this might cause differences in the average numbers obtained. We know now, however, that the number of vertebrae has been fixed long before 800 D°; but on the other hand it is still not obvious, how late in the development a very slight change in the number of fin-rays may be caused. When it is desired to see how e. g. the arches of the last vertebrae develop through the final stages of ossification, the fry may with advantage be fed for a time and thereby attain a more extensive ossification of the last vertebrae and their arches. As mentioned above I have, however, so far not fed the fry in the fundamental experiments, in order not to introduce unknown factors. Moreover I may here point out, that vertebrae and fin-rays of fry killed at about 800 D°, are fairly uniformly ossified, whether the fry has been kept in 3° or 6° or 9°.

The fry is killed by means of ether or chloroform and is placed in a shallow glass dish with 4 % neutralized formalin solution and with the specimens stretched out as far as possible.

The staining and clearing of the objects is of the greatest importance in order to obtain an accurate result by the countings. The staining technique and clearing of the objects employed during many years (Tåning 1927) has been somewhat altered owing to suggestions made by various experimenters (Hollister 1934, Raitt 1935) for improvement of the method, and the treatment in our experiments of about 100 specimens of fry has now been as follows:

After about three weeks of preservation in 4 % neutralized formalin, the sample is washed out in running water during 24 hours; it is then bleached by means of peroxide (about 20—30 cm³ to 500 cm³ distilled water); the sample ought during this process if possible to be exposed to sunlight and moreover kept at room-temperature, as the bleaching then takes place more quickly. When depigmentation has taken place the sample is transferred to distilled water, which is now and then renewed to get all the peroxide washed out. Then the sample may be placed in a vacuum in order to remove the last remnants of air in the tissue, and finally it is placed in 2 % potassium hydroxide for about 15—30 minutes.

The actual staining takes place in the following way:

To 500 cm³ distilled water is added 10 gram potassium hydroxide and to this is added ½ cm³ alizarine dye solution (1 cm³ glacial acetic acid + 2 cm³ glycerine + 12 cm³ 1 % chloral hydrat + about 0.3 gram of water-soluble alizarine (alizarine sodium sulphonate (Merck)), cf. Hollister 1934. The fry is immersed in the staining bath in a wide glass tube with canvas or silk bottom. Allowing for ordinary room-temperature the staining lasts about 24—48 hours. In order to clear the fry, the sample is removed directly from the staining bath to 2 % potassium hydroxide in which it is kept about 15—30 minutes. Then it is carried to a mixture of 50 % glycerine + 50 % 2 % potassium hydroxide, and is kept there for 24 hours. The sample is kept in a Petri-dish with glycerine at ordinary room-temperature for about 24 hours; the glycerine is changed 3 times.

Counting takes place by means of a microscope with movable stage. During the counting the specimens are covered with a glass slide in a square shallow glass dish containing glycerine. The staining has been so good, that cases of doubt regarding the number of vertebrae and fin-rays do not occur. By the counting of the individuals in an important series of samples, as e. g. the before mentioned H × G series, Leica-photographs have been taken of all special cases of fusions etc. of the vertebrae; contact copies or enlargements of these photographs have been used for a closer comparison of the more or less uniform types; by this procedure

I hope to have obtained a completely uniform judgement of the fusions in the pre-urostyle vertebrae and their arches. (These fusions have always been counted as 2 vertebrae, see on this, page 33 et seq.). Regarding the counting of the fin-rays it should be mentioned, that the last ray in the dorsal and anal fin, which is double, has been counted as 1; and as to the pectoral fin, it was nearly always the rays of the right fin which were counted.

In the tables p. 52 et seq. the frequency distributions of the vertebrae and fin-ray counts are given, together with the normal statistical constants of the counts. The thousands of detail countings can, however, not be included in this paper.

Besides the procedure mentioned regarding preservation, staining, counting etc. the majority of the samples has moreover been measured and weighed; 100 or more specimens from the samples have been measured, and weighing of 100 specimens has been carried out, in order to investigate the average weight of the individuals in the various series and samples incubated at different temperatures; this was made in order to see whether variation in size and weight might have any influence on certain results.

V. Experiments concerning the Influence of Temperature.

A. The Influence of high and low Temperatures on the average Number of Vertebrae and Fin-Rays of Sea-Trout.

1. The Number of Vertebrae.

In some of his well known experiments concerning racial investigations Schmidt (1921, p. 19—23) has proved, that eggs of Trout from the same parents incubated at various temperatures produce fry in which the average number of vertebrae is not only different, but that the difference due to temperature is this: fry incubated at both low and high temperatures (about 2° and 10°) has higher average values than fry incubated at intermediate temperatures (about 6—7°). I here refer only to Schmidt's experimental series 1 and 2, and not to series 3, the fry of which was incubated not in running water but in aerated water only (this series appeared, however, to behave just like the others, though with a certain dislocation of the values; see Schmidt 1921, fig. 7, and my fig. 5).

The experimental results left Schmidt somewhat puzzled, because it previously had been considered an almost established rule, that low temperatures in nature would give high average numbers of vertebrae, and high temperatures would give low average numbers of vertebrae. Schmidt intended later on to give a more detailed description of his experiments, but he was prevented in this by other investigations and various expeditions.

Kyle (1926 p. 192—193) mentions this experimental result and refer to it as "contradictory or paradoxical". As Kyle treats the experiment more in detail than it has been by others except Johnsen (1936) and furthermore attempts to give an explanation of it, we shall quote his statement (l. c. p. 193):

"The matter may perhaps be understood in the following manner. An increase of temperature undoubtedly heightens the metabolic processes and leads to greater activity internally. Thus, embryos are hatched out sooner under high temperatures, but are not so well-developed as under low; the larva is smaller with more yolk to be absorbed and the internal tissues are less differentiated. Hence, where a difference of temperature operates on the eggs, the higher

temperatures should lead to a smaller number of vertebræ. But the conditions are altered when the different temperatures operate on the hatched-out larvæ; the activity and movements of the latter have to be taken into account.

That the Trout hatched out under the lowest temperature should have the largest number of vertebræ is thus comprehensible, and it is possible that the highest temperature has so influenced the larvæ that they regained what they lost in the egg stage, that is by means of their own activity, so that they come to have a higher number of vertebræ than those under the intermediate temperatures, though they do not regain all that was lost by comparison with those that remained under the lowest temperatures all the time".

Fig. 5. Diagram showing the average numbers of vertebrae at low, intermediate and high temperatures. 1—3: SCHMIDT's results (see SCHMIDT, 1921, p. 21). 4—7: recent results from various pairs of Trout; 4: A×C; 5: B×D; 6: E×F; 7: G×H. Abscissae: temperatures at which incubation has taken place. Ordinates: fractions of a whole vertebra. See the text.

As it will be seen from the experiments mentioned later in this paper, the fixing of the final number of vertebrae is accomplished, however, long before the larva leaves the egg, and therefore KYLE's endeavour to give an explanation of the phenomenon does not hold good.

JOHNSEN (1936 p. 14) tries theoretically to find the cause of SCHMIDT's result in the fact, that water has the greatest specific gravity at 4° and concludes from the result of the experiment, that the average number of vertebrae decreases with increasing specific gravity. However, I shall not here go further into JOHNSEN's endeavour to explain the phenomenon, as it is still only a hypothesis, which experiments not yet have been able either to confirm or to reject. How the specific gravity of the water[1]) should already in the egg have the said influence on the fixation of the number of vertebrae is not easy to understand, and only experiments seem here to be likely to provide a solution. For the time being we have to work from the fact, that at any rate the temperature has an influence, whether it acts through the rising or falling chemical (possibly hormonal) reactions caused by its changes, or has some other unknown influence.

In order to be able to use the Sea-trout in experiments concerning the influence of the

[1]) Possibly the specific gravity of the perivitelline fluid, which seems to be very nearly that of the surrounding water.

environment on meristic characters, it was, however, necessary to investigate more closely the results obtained by SCHMIDT, and ascertain that we here had to deal with a fact, which we could treat as universally true for the matter in hand. This also has been proved by means of a series of experiments with a total of four different pairs of males and females, used in the years 1941—43. As shown in fig. 5 where these experiments as well as those of SCHMIDT's (Ser. 1—3) are included, we have always — apart from SCHMIDT's experiment no. 3 — the highest number of vertebrae at 2—4° and 8—10°, the lowest values at 6—7°. In my figure the lowest values have all been entered on the abscissa-axis, though these averages actually are different, determined as they are *inter alia* by the generative values of the parents.

Now as the results of so many experiments appear to correspond, it must be taken for granted, that we have here an established fact concerning Sea-trout under the experimental conditions used. When possible, however, also other experimental conditions and other species of fishes ought to be included in these investigations. I believe, however, that SCHMIDT has here found something of extraordinary interest, which I feel sure will be of importance, *inter alia*, for the theoretical exploration of the causal connection between the environmental factors and the variation of vertebrae. It is curious, that during the last more than twenty years since SCHMIDT's paper was issued, no attempts from other quarters have been made in order to elucidate or verify this very interesting experiment, and that only so few have mentioned SCHMIDT's results. VLADYKOV mentions in his summary "Environment and taxonomic characters of fishes" (1934 p. 107) this experiment, but not the specially remarkable facts, as he only observes: "A slight variation was observed in the number of vertebrae of fishes from the various lots. The greatest number of vertebrae occurred in those fishes which were subjected to the lowest temperature".

As shown in fig. 5, the size of the effect is very different even at similar or almost similar temperatures. The cause of this is apparently the special combination of personal and generative values in the individuals employed as parents. I add, that the effects in various samples of progeny from the same parents under uniform temperatures always have been found of practically the same size. The figure shows moreover, that the greatest effect most often occurs at the lowest temperatures, but that also the highest temperatures may give the greatest effect.

Through the investigations mentioned here, the foundation of the following experiments was determined with sufficient certainty, as in these experiments only temperatures between 2° and 10° were used, and thus we have not approached the threshold of development. The conditions at very low temperature are difficult to investigate, as the incubation at e. g. 1° will take about one year. At very high temperature hatching of eggs of Trout is difficult too, as then abnormalities very often occur, probably owing to the abnormal speed of development; hatching may, however, according to experiments made by others still be carried out at 14—15° C. (in case of Brook-trout even at 17°).

As similar experiments have still not been carried out with any other fish, it is not known, whether the average number of vertebrae in other species too will show high values both at particularly low and at particularly high temperatures, while intermediate temperatures give the lowest values. Probably e. g. arctic, boreal and tropic-subtropic species act differently in this respect. That the features in question have not generally been found in nature may be owing to the fact, that for instance the Trout will avoid the high temperatures, or that the fish is probably unable to spawn at these high temperatures, but that spawning can take place only within a certain limited interval of temperatures.

Through experiment alone we have any hope of getting a deeper knowledge of these problems; and a very interesting and fascinating work seems here to be in store for experimenters in marine fishes.

2. The Number of Rays in the dorsal, anal and pectoral Fins.

In the preceding chapter I have shown, that SCHMIDT's results regarding the influence of temperature on the number of vertebrae have been confirmed, and I shall now show, how low, intermediate and high temperatures influence the number of rays in the dorsal, anal and pectoral fins of the Sea-trout. I here use countings from the two pairs of Trout, the male G and the female H, and the male F and the female E. The result of the influence of temperature appeared to be the same for the fry of both pairs, which of course support the reliability of this result, probably applying to many species of fish. In our countings the last double ray in the dorsal and anal fins has, as mentioned, always been counted as one.

While there is no proof of any difference in the number of vertebrae, whether the sample has been preserved at 800 D° or not until some hundreds of day-degrees later, this evidently does not quite apply to the fins. Considering some samples from the series B and C (see tables 2 and 3, pp. 53—54) it will be seen, that several of the samples, which have been kept living about 200 D° longer than the other samples, show a slight increase in the average values.

	Series B (6°)		Series C (9°)	
Preserved at	800 D°	at 1046 D°	at 800 D°	at 999 D°
D	14.37	14.54	14.93	14.95
A	12.40	12.53	12.25	12.21
P	13.07	13.14	13.21	13.40

The cause of this is possibly, that the last developed ray in some cases is still not sufficiently ossified to be stained at 800 D°, while the staining at about 1000 D° owing to the more pronounced ossification gives slightly higher results. Further experiments may show, how late in the development such a slight change may possibly take place.

As, however, all the samples (of H × G and E × F) have been treated in the same way, and as the rise is only slight in the samples which lived beyond 800 D°, we shall in the following pages consider the results obtained from the uniform material preserved at 800 D°.

While we have shown that the average number of vertebrae is lowest at an intermediate temperature and highest at a lower as well as at a higher temperature, the facts are quite different regarding the number of rays in the fins mentioned. Fig. 6 shows this, and the curves for the average number of vertebrae from offspring of the two pairs of Trout mentioned have also been included for comparison.

The following table gives a survey of the results of the countings, details are to be found in the tables 1—5, p. 52 et seq.

	The average number of vertebrae		The average number of rays in:					
			Dorsal fin		Anal fin		Pectoral fin	
Series C°	H × G	E × F	H × G	E × F	H × G	E × F	H × G	E × F
C 9°	58.82	59.70	14.93	15.08	12.25	11.67	13.21	13.36
D 6°	58.55	59.17	14.66	14.80	12.56	11.92	13.13	13.13
B 6°	58.42	59.15	14.37	14.74	12.40	12.10	13.07	13.10
A 3°	58.89	59.49	14.06	14.03	12.55	11.86	12.64	12.64

From the figures and the tables the following will be seen. The average number of rays in the dorsal fin shows a steady increase from 3° over 6° to 9° with a rise of about one ray in this fin. In contrast to this the anal fin gives but a vague picture, the average number of rays in this fin varying only a little at the different temperatures, but it shows, however, a slight decrease at the highest temperature (9°). Finally the case is the same for the pectoral fin as for the dorsal fin, i. e. the lowest value at the lowest temperature, an intermediate value at 6°, and the highest value at the highest temperature. The increase is almost the same as in the case of the dorsal fin — a rise of 0.57—0.72; the various values for the offspring of the two pairs of Trout are strikingly alike, which, however, must be due to a mere chance, as they must be not only phenotypically but also genotypically determined.

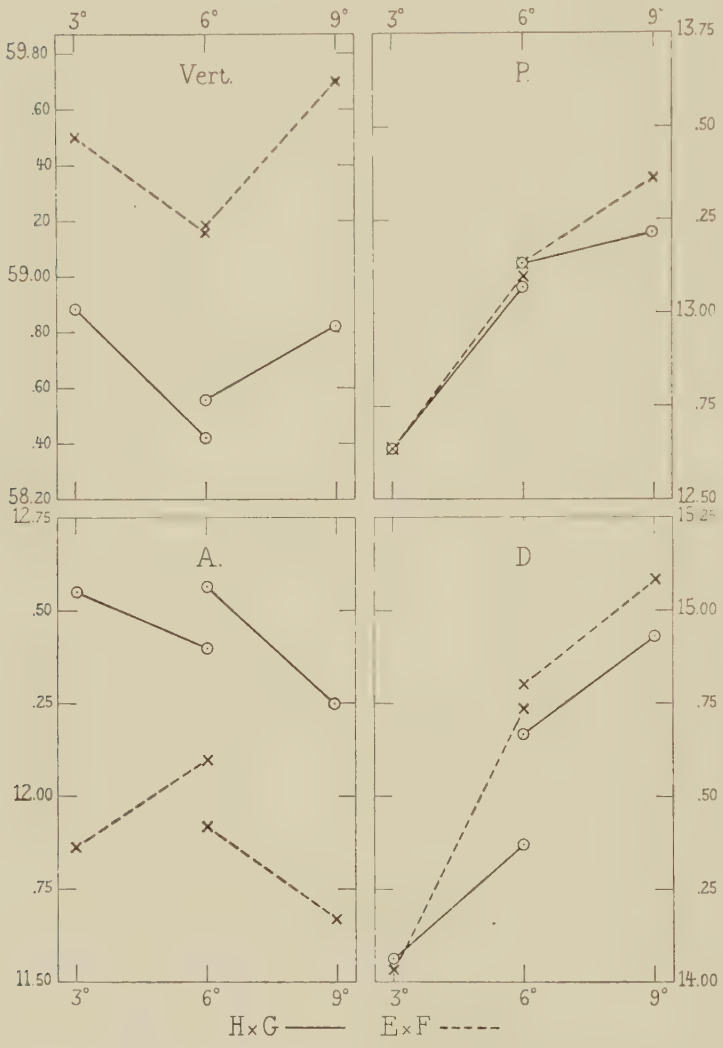

Fig. 6. The average values of vertebrae (Vert.) and of rays in the pectoral fin (P.), the anal fin (A.) and the dorsal fin (D.) obtained through development of Trout fry at 3°, 6° and 9°. Heavy lines connect averages from fry of H×G, the dotted lines from fry of E×F.

The results being almost identical for the two different series of fry, it is likely that the temperature factor in the case of Sea-trout generally produces such variations as these curves show.

The literature concerning variation in the number of rays of the paired and unpaired fins of various Teleosts shows that it has been difficult to find a general rule for this variation. An increasing number of vertebrae seems to be conditioned by low temperature and it is generally followed by an increasing number of rays in D and A; but conspicuous exceptions occur. It may e. g. be mentioned, that Schmidt (1917) experimentally has shown that the number of rays in the dorsal fin increases with rising temperatures in *Lebistes*, and Leonard P. Schultz (1926) shows that the same applies to the number of rays in the anal fin in *Notemigonus* from North America; finally it may be mentioned that A. J. C. Jensen (1939) has shown an increase of the number of rays in the anal fin of Plaice (*Pleuronectes platessa*) and Dab (*Limanda limanda*) at rising temperatures (0.4 ray at the rise of 1°). As for the pectoral fin the upshot is no better. The matter is moreover complicated owing to the fact, that a change

in the temperature during development, as we shall see below, need not be followed by an effect at low temperatures, while at higher temperatures it may cause a pronounced effect. Different facts seem to show, however, that variations occur from one species to another or perhaps from one group of species to another in accordance with the localisation of the developmental period of the various fins during the ontogeny. The different transfers from one temperature to another, which I have carried out, produce, however, material for some understanding of the importance of temperature to the variation of the number of fin rays in the Sea-trout, and in what stage of development the influence is strongest; as to this, see p. 28.

B. The Fixation-Period of some meristic Characters in Sea-Trout.

1. The Vertebrae.

The moment when the final number of vertebrae of a Teleost is fixed, has not, so far as is known to me, been subject to experimental investigations until quite recent years. Some scientists have considered the final average number of vertebrae genetically determined, viz. at the moment of fertilisation; others have thought that the fixation-period chiefly must be identified with the period, when the centra just can be seen formed in the tip of the tail of the tiny postlarva. And various other opinions lie between these two extremes. In the following lines I shall quote some passages from defenders of the extreme opinions.

The view of some scientists is expressed by H. M. Kyle (1923 p. 3): "In the fishes, however, the segmentation of the body, though it may begin in the egg, is not completed until a varying time after the larva has escaped". And further (l. c. p. 5): "No data have been specially collected on this point (i. e. the size or length when the vertebrae have just been formed), but the segmentation is completed, when the hypurals have been formed, or rather, to be more precise, a little earlier when the notochord has been bent upward. Regarding this a good deal of information, though admittedly not absolutely exact, is already available."[1]) Then Kyle gives the size alluded to for a number of fishes (species, genera and families) and arranges these data in relation to the number of vertebrae in a table, the groups of which have a range from 5 to > 20 mm., and which in the fish species and groups dealt with shows an increasing number of vertebrae corresponding to the stage of development mentioned; and Kyle then finds a progressive increase in the number of vertebrae from 25 to > 60 parallel to the size of the larvae precisely in the stage of development mentioned.

Later in the same paper Kyle mentions his special theory, that it is the movements of the fry which causes the breaking up of the chorda in the vertebrae — a theory which has met with some opposition — and he says (l. c. p. 7): "Whatever it may be that gives the first stimulus, it is the movements of the fish, beginning in the egg and continuing in the free-swimming life, which lead to the segmentation of the primordial substance, each segment being comparable to the particles of an undulation in wave-motion. And it is the balance of the fish, the proportion between head and body, which determines the number of segments or vertebrae." .... "The greater proportion of the vertebrae, thus, excluding the variation of the individual or species, are fixed by the inherited distribution or balance of the primordial substance." And in his hand-book "The Biology of Fishes", 1926, p. 81, Kyle gives the fol-

[1]) I must, however, remark that the number of myotomes almost exactly corresponding to the final number of vertebrae can nearly always be counted in the embryos near the time of hatching in the case of most fishes in northern seas, i. e. some time before the tip of the notochord has been bent upward.

lowing survey of what he supposes takes place: "For a long time after the young Teleost is hatched, the notochordal tube is straight and its walls become slightly ossified in the same way as the small bones. Then the movements of the muscles lead to its breaking up into segments or centra, each between a pair of muscles. Ossification ceases in the parts between the centra where they are working on each other, and thus the whole axis comes to have the appearance of a long series of small tubes or cylinders, most clearly seen in any postlarval Clupeid. The number of these cylinders in any species is not determined until the little fish has been moving about for some time. In the Teleosts, therefore, the number is determined under the combined influences of the movements and the outer conditions."

KYLE undoubtedly assumes, that when he (for instance in the postlarval Herring) has not been able to see the last vertebrae distinctly developed by means of the microscope and staining methods, then they were not formed or their number fixed.

I shall then mention an opinion totally different from KYLE's and from a paper more recent than his — that of SCHNAKENBECK (1931), who in many points is opposed to KYLE's special theory of the development of the vertebrae (p. 432). SCHNAKENBECK considers the number of vertebrae to be genetically determined, and he is of the opinion that the mechanism of the development — from the time of the formation of the embryo until the larva shows the final metameristic characters — does not offer any opportunity for any external influence. In the paper referred to (p. 475—76) it may clearly be seen from SCHNAKENBECK's survey of the hydrographical conditions in which the young Herring is developed in the North Sea, that he pictures the Herring fry hatched and floating in the surface of the water before the characters have been fully developed; and he says here (p. 476) *inter alia*: "Es ergibt sich also unter Berücksichtigung durchschnittlicher Temperaturen, daß einerseits die kritischen Entwicklungsphasen[1]) einer einzigen Rasse sehr verschiedenen Temperaturen (Schwankungen bis zu durchschnittlich 10°) ausgesetzt sind, daß aber andererseits kritische Entwicklungsphasen von zwei verschiedenen Rassen teilweise den gleichen Temperaturen ausgesetzt sind." He is therefore of the opinion, that the race-characters of e. g. the Channel- and the Bankherring must be genotypically determined, and not phenotypically determined by e. g. the temperature, which in the last case would obliterate all differences. This conclusion must be accepted, provided the most important race-character of the two forms of Herring mentioned, viz. the number of vertebrae, was not fully fixed until the larva had been hatched out and was floating in the surface; but the case is different if an influence makes itself felt predominantly during the very early stages of the egg, when the temperatures prevailing at the bottom, where the egg is deposited, vary within narrow limits, and when the temperature on the spawning grounds of the two Herring races mentioned only rarely show an overlapping during the period of propagation.

The view, which during recent years seems to be adopted by many fishery biologists, we find expressed by DAVIS (1936 p. 12) at the Lowestoft meeting concerning Herring investigations: "I believe that the physical distinguishing marks of communities are laid down during the plastic period before the hard parts peculiar to the adult are formed, and are subject to the varied modifying influences of the area in which this plastic period is spent."

It is noticeable, that no definite opinion has been expressed as to the exact period during the ontogeny when the fixation takes place; only that it must take place previous to the ossification.

[1]) "die kritische Entwicklungszeit" has been defined loc. cit. p. 475 as "die Zeit, in der die als Rassenmerkmale benutzten Eigenschaften noch nicht alle voll ausgebildet sind und demnach auf äussere Einflüsse reagieren könnten, . . .".

At the beginning of this chapter (p. 19) I mentioned, that experiments concerning this matter were not initiated until quite recently; this refers to a brief statement by GUNNAR ROLLEFSEN in "Naturen" June - July 1940 where it is stated, that the number of vertebrae and fin-rays in the fry of the Flounder seems to depend on the temperature to which the fry has been exposed during the first 8—14 days after hatching. Unfortunately present circumstances have rendered it impossible for ROLLEFSEN to continue his interesting investigations into the rearing of fry of flat-fishes with *Artemia* as food by which experiments of far reaching importance will be made possible. ROLLEFSEN's experiments have, however, not yet been published in detail, but we may look forward to the details with high expectations, because it will be of much interest to compare the results obtained with two teleostean fishes so widely different taxonomically and biologically as the Flounder and the Sea-trout.

The question which I shall now endeavour to elucidate in this chapter is, whether, in the case of the Sea-trout, it can be experimentally determined at what period during ontogeny it is possible by a change of temperature so to influence the egg, the embryo or the larva, that the individual adopts another number of vertebrae than it would have done otherwise, if the development had continued under the temperature at which the development commenced. In other words, I shall endeavour to determine the period in which the fixation of the final number of vertebrae takes place in the case of the Sea-trout. I will, however, not here consider the possible influence of other environmental factors than the temperature.

Concerning the fixation-period of other morphological characters it clearly appears from previous experiences in nature, that characters like the number of fin rays in the dorsal, anal and pectoral fins have fixation-periods different from those of the vertebrae.

SCHMIDT already pointed out that the various meristic characters do not correspond in their increase or decrease, and I shall here, *inter alia*, also mention that A. J. C. JENSEN recently (1939) has been able to show, that even one of the unpaired fins, viz. the anal fin of Plaice and Dab, does not follow the number of vertebrae; a rise of the temperature of 1° C involves an increase of 0.4 in the number of rays in the anal fin; moreover it is assumed (p. 378), that the influence takes place in the first or second week after the hatching.

In order to elucidate the question of the period during the ontogeny when the number of vertebrae of the Sea-trout is determined, I shall preferably in the following use the experimental series H × G from 1942—43; various points concerning the matter may, however, be further elucidated by means of some other series, which have been included in the experimental work of recent years. The principle of the experiments has been to transfer batches of eggs in various stages of development from one temperature to another and then determine the meristic values, which the fry had attained when fully developed.

As SCHMIDT's experiments and my recent repetitions of them had proved, that eggs kept at 3° as well as at 9° produced fry with a high average number of vertebrae, while eggs at 6° produced a low average number, I hoped by transferring the samples at various stages of development — from e. g. a low temperature to an intermediate temperature — to be able to ascertain the period in which the fixing of the final number of vertebrae had taken place.

The object of the investigation was accordingly to enter the mean values obtained through experiments on a curve as given in fig. 7, p. 22. We assume that in this curve the mean

value of the number of vertebrae is determined for many samples, which gradually — i. e. after an increasing number of day-degrees — have been transferred from one large sample of eggs kept at a certain temperature, e. g. 3°, to a series with another temperature, e. g. 6°. The first samples which are transferred will all adopt the same mean value as the control sample developed at 6°; but at some moment or other a change will take place, and all the samples transferred later than a certain period will then retain the same mean value as the control sample developed at 3°. The object is therefore to make an attempt to ascertain when the change takes place in relation to the number of day-degrees elapsed (the number of day-degrees giving the age of the embryo), and moreover to decide whether the change takes place suddenly or gradually.

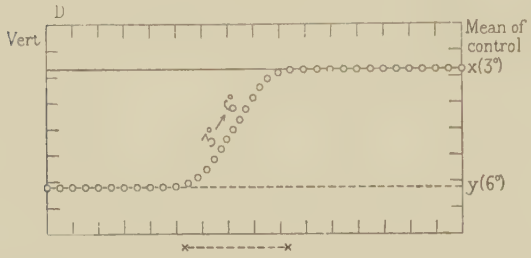

Fig. 7. Theoretical curve showing results of transfers. ooooo: Situation of the means obtained from transfers. x: mean of control at 3°; y: the same at 6°. x - - - - x: theoretical fixation-period of the number of vertebrae. See the text p. 21—22.

According to my knowledge of the opinions of various authors about the moment of the fixation of vertebrae in Teleosts, I supposed that it took place late during the development of the egg or during the larval development, and that the embryo at any rate would be so far developed, that its caudal part was far advanced in development. It seemed therefore very probable, that in the case of the Trout we had to find the moment of fixation in the period between the pigmentation of the eye and the hatching, at which latter moment the notochord has passed through the greater part of the development, which includes the bending up of the tip of the notochord, and which leads to the final form of the tail. As we shall see later on, I was wrong in my judgement of the moment of fixation.

In keeping with my assumptions, transfers were made in the four series in three periods: 1) in the period immediately previous to the pigmentation in the eye being visible, 2) in the period between the young eyed-egg stage and the hatching, and finally 3) in the period shortly after the hatching of the larva. These stages will be seen in fig. 3, p. 8. In each of the four series a batch of eggs remained as controls under the same temperature throughout its development until the preservation took place.

As mentioned above, the number of day-degrees (D°) is used as the criterion most adaptable for the determination of the moment of the transfers carried out; and from fig. 8a—b, p. 23, the sequence and moments of the transfers will be seen. The number of day-degrees and of days after the fertilisation is given for the moment when the transfers took place. Moreover, the actual average temperature for the period previous to and after the transfer has been entered in the figure. Finally the average numbers of vertebrae and fin-rays for each of the samples are seen to the right in the figure.

From fig. 8 and the tables it will now be seen, that transfers from one temperature to another have been carried out at the following number of day-degrees: 1) previous to or just at the beginning of the eyed-egg stage: at 142, 155, 168, and 191 D°; 2) in the stage between the young eyed-egg stage and the hatching: at 215, 242, 275, 299 and 358 D°; 3) after the hatching: at 425, 442, and 466 D°. As mentioned elsewhere the eyed-egg stage is reached about 200 D°, and the hatching takes place at about 400 D°.

The results of the countings of the vertebrae are to be found partly in the tables p. 52 et seq., partly in the figures given (figs. 8—13). The tables need no further explanation than

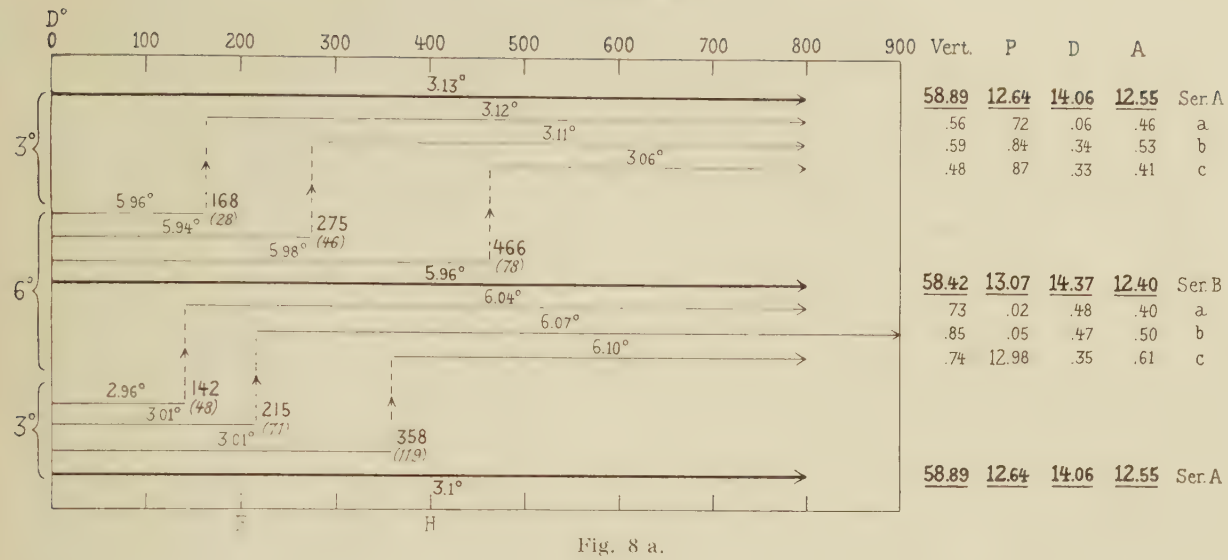

Fig. 8 a.

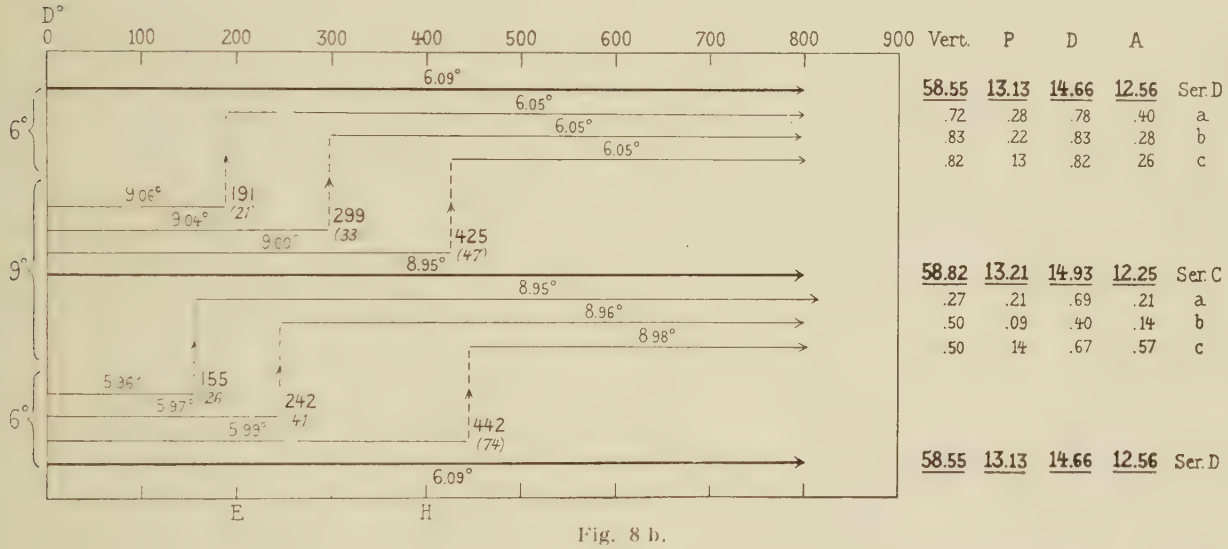

Fig. 8 b.

Fig. 8a and b. Diagrams showing the transfers of samples carried out between the temperatures 3° and 6° and between 6° and 9°. To the right the average numbers of vertebrae and fin rays (the heavy figures indicate controls). D° = day-degrees. E = eyed-egg stage. H = hatching. Average temperature entered for the period previous to and after the transfer. Heavy lines indicate the controls. The number of day-degrees and of days (in parenthesis) indicated at each moment of transfer.

that given p. 57. The frequency polygons with the average number of vertebrae entered gives, however, a more perspicuous picture than the tables; in each of the figures the control samples are placed above and below the polygons of the samples transferred. The arrows with the figures, which indicate the moment of transfer in day-degrees, point towards the temperature to which the transfer has taken place. By this arrangement of the curves it is easy to see, whether changes in the number of vertebrae have taken place owing to the transfer from one series to another. Finally fig. 13, p. 28 shows the situation of the mean values of the samples

transferred in relation to the mean values of the control samples. The mean values of the samples transferred are entered in the graph in relation to the moment of their transfer (specified in day-degrees).

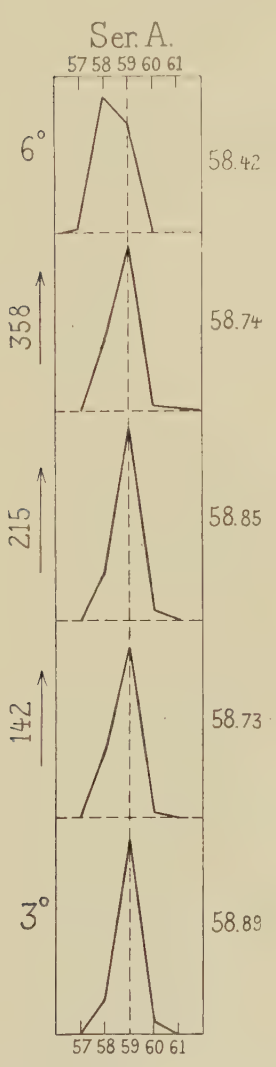

Fig. 9.

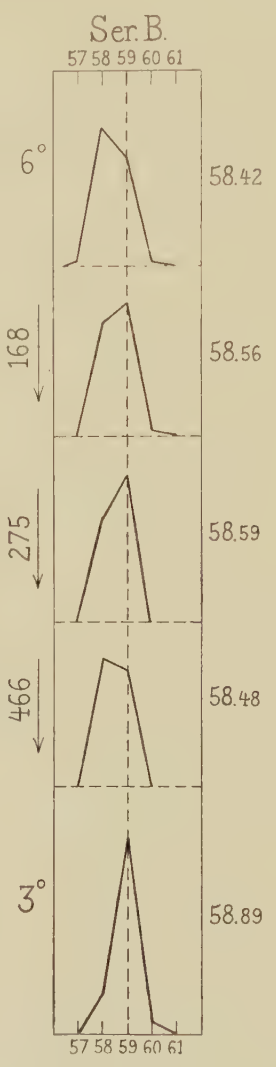

Fig. 10.

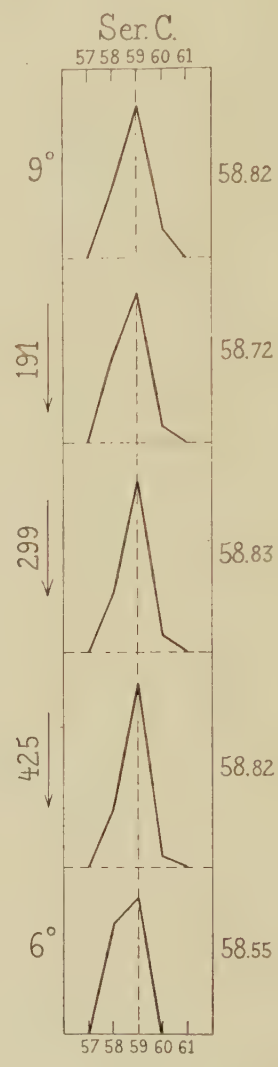

Fig. 11.

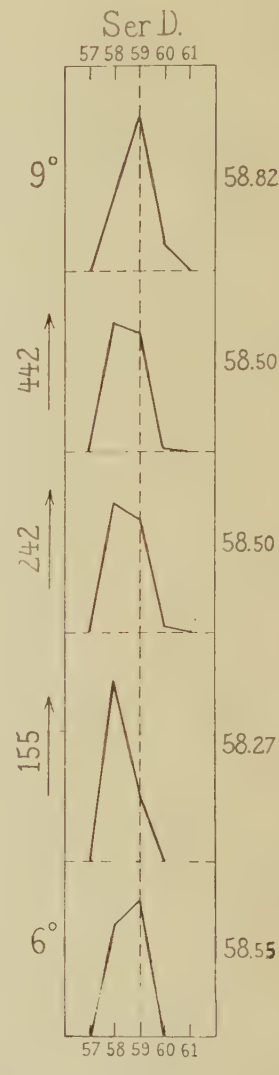

Fig. 12.

Fig. 9. Percentage frequency polygons illustrating the results of countings of vertebrae from the series A (transfers from 3° to 6°). At the top and at the bottom the two controls. To the left: the moment in day-degrees when transfers were carried out. The arrows show the direction of the transfer in relation to controls. To the right: vertebral averages of the various samples. See the text p. 25.

Fig. 10. Frequency polygons illustrating the results from countings of vertebrae from the series B (transfers from 6° to 3°). See the text p. 25.

Fig. 11. Frequency polygons illustrating the results from countings of vertebrae from the series C (tranfers from 9° to 6°). See the text p. 26.

Fig. 12. Frequency polygons illustrating the results from countings of vertebrae from the series D (transfers from 6° to 9°). See the text p. 26.

Series A. 3° — transfer to 6°.

In this series the three samples were transferred from 3° to 6° after 48 days, 71 days and 119 days (or at 142, 215 and 358 day-degrees).

The control sample for the 3° series shows an average number of vertebrae of **58.89,** while the control sample for the 6° series shows **58.42.** As the three samples transferred show 58.73, 58.85 and 58.74 respectively, no significant change has taken place in the average number of vertebrae after the transfer (see figs. 9 and 13).

That the second sample shows a number a little higher than the two other samples might possibly be explained from the fact, that the preservation of this sample was postponed for the sake of experiment, until about 900 day-degrees had elapsed, while in all other cases the preservation took place at about 800 D°. And it might then be supposed that some less prominent pre-urostyle fusions owing to the more advanced ossification would have been more easy to observe; the number of observed pre-urostyle fusions in the samples is, however, 11, 9 and 16 respectively, and accordingly we have just the lowest numbers in the sample mentioned. That the two other samples have a rather low average number of vertebrae — and therefore seems to approach the value in the control sample for 6° — may possibly be considered as a mere chance, as even the lowest value is not significantly different from the mean value of the control sample for 3°; as to this question see, however, also p. 38 et seq. on fused vertebrae.

In order to investigate whether the effect of a shock might change the number of vertebrae of the individuals in series A, a sample was transferred after 213 day-degrees from 3° to 9° (i e. just at the moment when the pigmentation of the eye commenced to be visible from without). No change could, however, be traced in the average number of vertebrae, the sample having an average of 58.84 (in the control sample A at 3°: 58.89, and in the control sample C at 9°: 58.82). The countings etc. from the sample are to be found in Table 1 p. 52.

Series B. 6° — transfer to 3°.

In this series the three samples were transferred from 6° to 3° after 28, 46 and 78 days respectively (or at 168, 275 and 466 day-degrees).

The control samples were the same as in the preceding series and show for the 6°-series an average number of vertebrae of **58.42,** while the control sample for the 3°-series gave **58.89.** The three samples transferred had the following means: 58.56, 58.59 and 58.48, and it is obvious that no significant change of averages has been obtained (see figs. 10 and 13).

The sample which was influenced by a temperature of 6° for the longest period had a mean corresponding very closely to the mean of the control sample, while the means of the other two samples were a little higher; the slight difference may probably be insignificant, but as to this, see p. 38 et seq. on fused vertebrae.

The main result from this series is at any rate sufficiently clear, and the deviations observed can be explained only through much more elaborate experiments; possibly, however, the deviations are quite insignificant.

We may here add, that the control sample for this series was divided into two samples of which one was preserved at 798 D°, the other at 1046 D°; the number of vertebrae for the first was as mentioned 58.42 and for the second exactly the same, viz. 58.41 (the number of pre-urostyle fusions differed only slightly, being 11 and 15 respectively, see table 2, p. 53).

Series C. 9° — transfer to 6°.

We have now in the preceding two series considered samples developed under low or intermediate temperatures; in this series and the following the samples will have passed through their development under high or intermediate temperatures.

In the present series the three samples were transferred from 9° to 6° after 21, 33 and 47 days respectively (or at 191, 299 and 425 D°).

The control sample for the 9°-series has an average number of vertebrae of **58.82,** while the control sample for the 6°-series in this case shows **58.55;** the difference between these two samples is thus small. The three samples transferred show the following number of vertebrae: 58.72, 58.83 and 58.82, i. e. averages lying very close to the mean of the control sample in the 9°-series. (See figs. 11 and 13).

A calculation of the probable error of the difference shows, however, that the sample first transferred is not significantly different from the control sample at 6°, and it is accordingly impossible to see if the value is a casual effect or in reality shows a tendency to be equal to the value of the control sample at 6°. It is therefore a little uncertain, whether the number of vertebrae had been completely fixed previous to the earliest transfer (at 191 D°, see p. 38).

In order to try whether the effect of a shock was able to change the number of vertebrae, if fry recently hatched was suddenly transferred from a high to a low temperature, a sample was transferred after 432 day-degrees from 9° to 3°; no effect was seen as the average turned out to be 58.74 as against 58.82 in the control sample (see moreover table 3 p. 54); and this result agrees very well with our general results obtained.

In order to investigate, as we have done in some other series, whether the results of the countings remain the same though the age of the fry is greater than usually, a sample of this series was not preserved until after 999 D°; it showed 58.79 as against 58.82 in the control sample. This result confirms accordingly, that the number of vertebrae of the sample may as safely be counted when 800 D° old as when 1000 D°.

Series D. 6° — transfer to 9°.

In this series the three samples were transferred from 6° to 9° after 26, 41 and 74 days respectively (or 155, 242 and 442 day-degrees).

The control samples are the same as in series C and show for 6°: **58.55,** and for 9°: **58.82.** It is worth noticing here, that the control sample in the other 6°-series (B) has almost the same value as this series, viz. 58.42; the two systems accordingly correspond as well as may be expected, because full conformity in temperature in the two distinct systems cannot be obtained from day to day during so long a period as is the case here. The three samples in the series transferred gave 58.27, 58.50 and 58.50 respectively. The percentage curves are seen in fig. 12; see moreover fig. 13.

The sample transferred first (at 155 D°) gave 58.27 as average number of vertebrae, and it is conspicuously different from the control sample in the series from which it derives, viz. 0.28 lower, and still more from the control sample of the 9°-series, viz. 0.51. Owing to the fact that the sample ("a" in table 4 p. 55) alone among all those transferred showed so great a difference from the controls, another sample of 100 specimens was counted. The result was a mean of 58.21, which is the same as the first average obtained (see table 4). If the two samples counted (from "a", 155 D°) are added, we get an average of 58.24, which according to the probable error of the difference deviates significantly from the averages of the two other samples transferred in this series. Thus there can be no doubt, that as regards this sample a change

in the number of vertebrae has taken place, but in such a way that it has become still lower than the number of the control sample D at 6°[1]), and it has not at all approached the mean of the 9°-series. I therefore suppose, that this sample has either been exposed to an undetectable influence in one or another period of the development (a shock or some other influence, which has not been noticed) or the sample has been transferred just in a very sensitive period, and therefore owing to the effect of some shock through the sudden transfer to a higher temperature has reacted in such a way that the average number of vertebrae has become lower. To the latter supposition it may be objected, that in the series A (3°) a transfer was made at only 142 day-degrees, which does not show any significant change of the average, though the transfer took place a little earlier than that of the present sample. The difference between the numbers of day-degrees for the two samples is, however, only 13 D° (155 ÷ 142), provided the zero point of the Celsius thermometer is taken as threshold value; but as the development at 3° and 6° hardly, as mentioned before, correspond completely at the same number of day-degrees (with 0° Celsius as threshold value) there is a possibility that the sample of the A-series already had passed the sensitive period, while the sample of the D-series was still in this period[2]). Moreover there is also the possibility, that the higher temperatures, which the samples of the D-series were exposed to in this period, have an effect different from that of the lower temperatures, in which the samples of the A-series were placed.

However this may be, the main point is evident, viz. that an influence has made itself felt, but opposite to that which might be expected. Probably we are here approaching to the number of day-degrees when the fixation-period for the number of vertebrae will be found, but only further experiments can establish the limits of this period and settle the matter.

As to the other two samples, which were transferred in this series (at 242 and 442 D°) they are exactly like the 6°-control as regards the number of vertebrae; and any change towards the higher number of vertebrae in the 9°-series has not taken place in the case of any of the three samples transferred.

Transfers within the various series took place as mentioned above at the following moments, which are given below in days and in day-degrees.

A:	3° (→ 6°):	Days:	**48**	**71**	**119**	3° (→ 9°):	**71**
		D°:	142	215	358		213
B:	6° (→ 3°):	Days:	**28**	**46**	**78**		
		D°:	168	275	466		
C:	9° (→ 6°):	Days:	**21**	**33**	**47**	9° (→ 3°):	**48**
		D°:	191	299	425		432
D:	6° (→ 9°):	Days:	**26**	**41**	**74**		
		D°:	155	242	442		

[1]) Moreover it shall be mentioned here, that the number of pre-urostyle fusions in the low variates of vertebrae (57—58) are much greater in this sample than in all the other samples; of a total of 15 fusions in 921 individuals with 58 vertebrae, no less than 5 are from this sample, which accordingly has 3.3 % fusions on this vertebrae class as against 1.3 % in all the other samples together.

[2]) If for instance the threshold value (the biological zero) for the development of eggs of Trout is situated at ÷ 0.55°, the age in number of day-degrees of the two samples considered is the same when transferred, viz. 170 D°, and at a still lower threshold value the series A-embryos will be older than the series D-embryos counted in day-degrees. The threshold value for the development of the egg of the Trout is, however, a mere theoretical value, as hatching of course cannot be carried out in fresh water below 0° C.

Considering now the several results obtained from the transfers in the series A, B, C and D, it will be seen, that during the long period from the end of about 150 day-degrees until the fry is hatched out and has attained an age of about 800—1000 day-degrees, it has not been possible to change the number of vertebrae significantly, and accordingly the fixation of the final number of vertebrae must take place at an earlier stage of the development, that is considerably previous to the eyed-egg stage. The result of the experimental series D might, however, indicate, that the end of the fixation-period is possibly situated a short time previous to or quite close upon the stage of development which is reached after about 25—26 days at 6° C. (at about 150 D°). This corresponds to the stage during the development of the embryo, when the preformation of the last vertebrae takes place, viz. as the most posterior mesoderm segments. The sketch fig. 3 (144) p. 8 shows this stage.

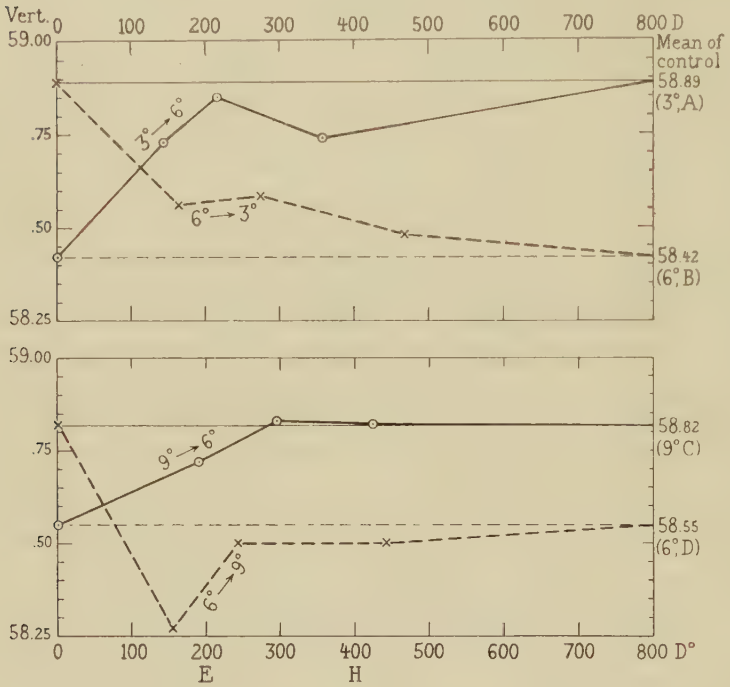

Fig. 13. The situation of the average number of vertebrae in the samples transferred in relation to the means of controls. Cf. fig. 8 and the text.

As mentioned above and as appears from e. g. fig. 13 it is possible that a very slight change may take place during the period after about 150 D°; such a minor change is undoubtedly caused by a slight alteration within the pre-urostyle vertebrae, a subject which we shall return to later in this paper, p. 32 et seq.

2. The Rays in the dorsal, anal and pectoral Fins.

As already referred to, the fixation-period for the number of rays in the fins that we have examined ends later than in the case of the vertebrae; this must be regarded as a natural consequence of the situation during the ontogeny of the periods in which these characters are developed. But it must be emphasized, that the laws controling the variation of these characters are evidently more difficult to detect than in the case of the vertebrae; to this contributes the fact, that these characters seem more unstable, more open to influence, than the vertebrae and have a later and longer fixation-period. The available material is, however, still too scant to afford a correct picture of the conditions; the influence of other temperatures than those employed must, *inter alia*, be used in the experiments, and transfers also be carried out during the development later than it has so far been possible. As in case of the vertebrae, experiments ought moreover to be carried out with variation also of other environmental factors, before the laws of influences in the case of this species may possibly be found. I shall therefore here

only point out some few results achieved through the experimental transfers carried out so far, using curves drawn as perspicuously as possible, given the present limited material.

In order to show in a diagrammatic representation the moments for the transfers, the average temperatures etc., I refer to fig. 8, which also includes the various means of the dorsal, anal and pectoral fins, and of the vertebrae too. The average values are moreover given graphically in figs. 14—16; details as to the countings are to be found in the tables 1—4 pp. 52—55.

It should be mentioned here, that the rays in the fins investigated at hatching time (about 400 D°) are still very far from being so developed, that they can be counted. In the middle of the dorsal and anal fin the rays begin to be faintly visible, while they are quite indistinct in the anterior and posterior part of these fins. In the pectoral fin the development of the rays proceeds from the anterior to the posterior (ventral) part, but has still not commenced when hatching occurs. No deposit of calcium seems to have taken place in the fins mentioned even at the time of hatching, or it has at any rate been so slight, that the staining method used has given no distinct reaction. It is not long, however, before a deposit of calcium begins to take place in the fin rays.

Detailed studies of the embryonic development might surely in numerous cases contribute to elucidate various conditions of importance for the experiments in question. I shall here for instance

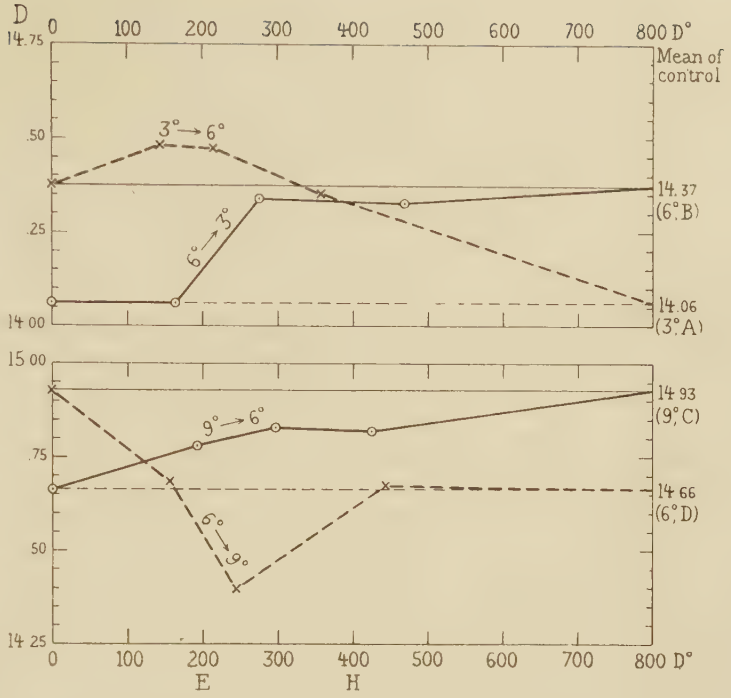

Fig. 14. The situation of the average number of dorsal-rays in the samples transferred in relation to the means of controls. Cf. fig. 8 and the text.

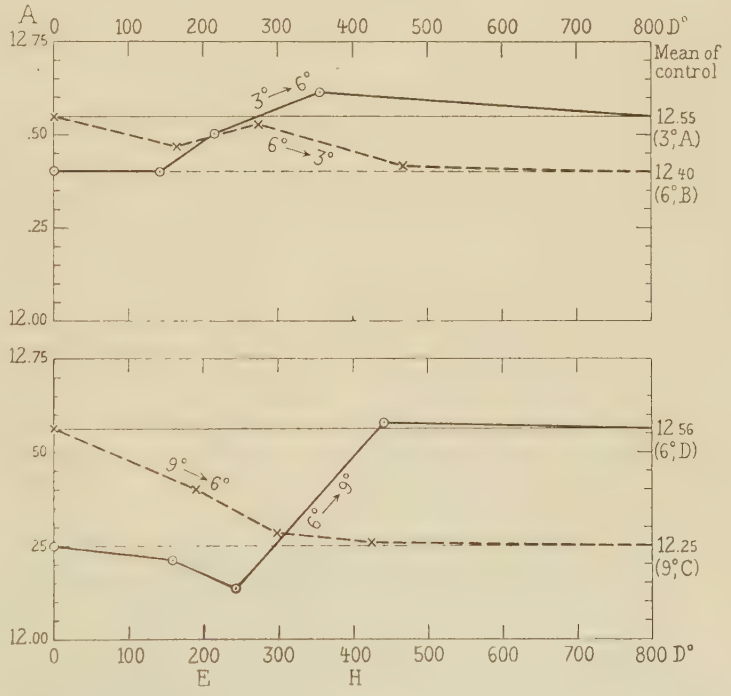

Fig. 15. The situation of the average number of anal-rays in the samples transferred in relation to the means of controls. Cf. fig. 8 and the text.

call attention to the fact, that increase or decrease of rays in the unpaired fins must take place in the anterior part of these fins. Thus HARRISON (1894—1895) has pointed out, that in case of *Salmo salar* "The segmentation of the extreme anterior portion of the fins is secondary, although in the adult no difference can be seen between the two portions" (1894 p. 42). In the pectoral fin — the origin and embryonic development of which differ not a little from those of the dorsal and anal fins — the last rays are, however, as mentioned developed in the posterior (ventral) part of the fin.

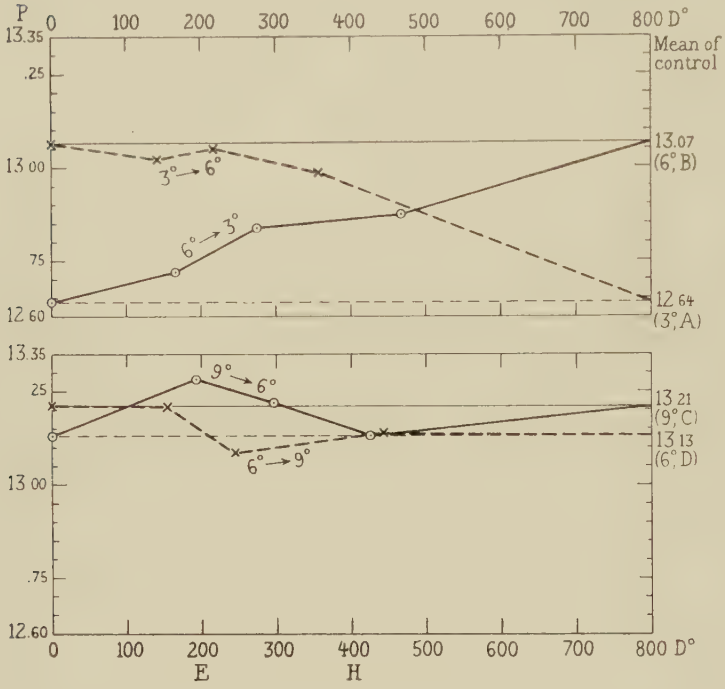

Fig. 16. The situation of the average number of pectoral-rays in the samples transferred in relation to the means of controls. Cf. fig. 8 and the text.

The curves in figs. 14—16 give a survey of the results obtained from the transfers in the main series. As to the remaining few results, e. g. transfers from 3° to 9° and *vice versa*, we shall refer to the tables (nos. 1 p. 52, 3 p. 54 and 5 p. 56); the results obtained hereby support those drawn from the main series.

From the accessible material it appears that in some cases there have been quite unexpected effects as to which we can, so far, observe only that possibly the cause of these is to be found in our lack of complete control over all the environmental factors, or that it may be due to unnoticed accidents occurring during the transfers, or finally to the fact, that the individuals were in a particularly sensitive period.

Moreover several of the transfers give no significant results, because the difference between the control samples is so slight, that it is impossible to prove anything statistically; this is true to a certain degree for the results obtained from the dorsal and pectoral fins at the high temperatures and from the anal fin at the low temperatures. Possibly in this connection it is of some importance if the effective temperature during development is high or low.

Then it may be observed, that the period in which a change may take place is evidently of long duration, and not a quite short period. This is particularly conspicuous in the case of the pectoral fin, which may be subject to influence from the young eyed-egg stage during the long period possibly ending at about 1000 D° or even somewhat later.

It seems that the chief effects of the temperature on the anal and dorsal fins occur before hatching (400 D°); in the case of the anal fin, the effect makes itself felt mainly before 300 D°; in the case of the dorsal fin, the effect is operative during a longer period, but is of a more unstable nature.

Finally I shall call attention to a characteristic feature, illustrated in the curves fig. 17, where the results concerning the dorsal and the pectoral fins are included in the same co-

ordinate system. It is evident, that there is a close correlation between the values obtained from these two fins (with the exception of the results from the transfer from 9° to 6°) in spite of the fact, that the progress of development in these two fins is rather different. As previously pointed out (p. 18) these two fins both show an increasing average number of rays at rising temperature and it is therefore interesting to notice, that such a parallelism manifests itself even in the case of transfers carried out from higher temperatures to lower as well as *vice versa*.

This close correlation may also be noticed outside the samples of the main series, viz. in offspring of two different pairs of Trout (H × G and E × F) transferred from 3° to 9°. I shall here particularly call attention to the correlation between the values from the pectoral fin and partly too the dorsal fin in the offspring of these different parents. See the following table.

Average value for		3° Control	Transfers from 3° to 9°	9° Control
P	H × G.....	**12.64**[1])	**12.93**[1])	**13.21**[3])
	E × F.....	**12.64**[2])	**12.93**[2])	**13.36**[4])
D	H × G.....	**14.06**[1])	**14.66**[1])	**14.93**[3])
	E × F.....	**14.03**[2])	**14.42**[2])	**15.08**[4])

[1]) Transfer at 213 D°, see table 1, p. 52.
[2]) Transfer at 279 D°, see table 5, p. 56.
[3]) See table 3, p. 54.
[4]) See table 5, p. 56.

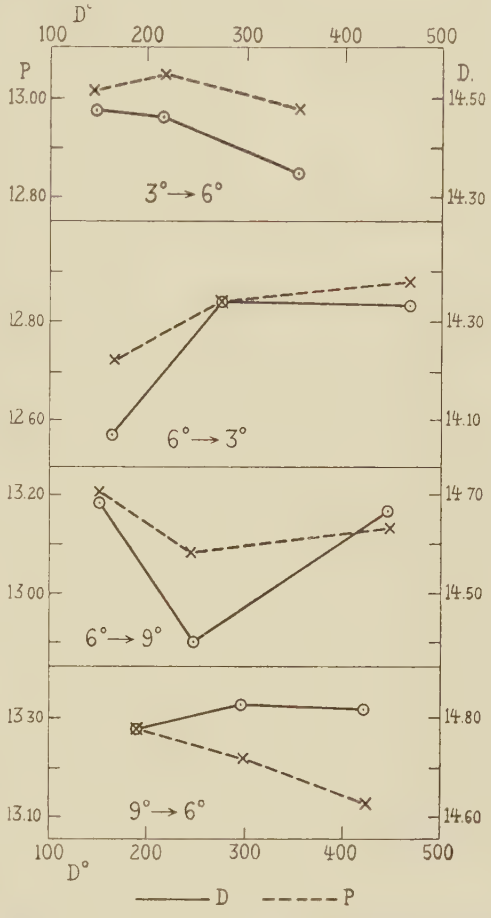

Fig. 17. Correlation of the average numbers of the dorsal-rays (D.) and the pectoral-rays (P.) in transfers; see the text.

It will be necessary in future to carry out closer investigation of the feature pointed out here, as no suitable interpretation seems to be forth-coming so far.

It seems to emerge from the few experiments as yet carried out, that the conditions regarding the periods for the fixation of the number of rays in D, A and P are rather complicated. There can, however, be no doubt, that already very early in the development, previous to or in the eyed-egg stage, there is in several cases some reluctance to desert the values first induced. But on the other hand some influence may produce an effect, though very slight, on the embryo rather late in its development; in the case of A and D, however, only in the stage previous to the complete absorption of the yolk. By means of further experimental results there may be hope, however, of elucidating these questions; and in spite of our very limited conclusions these first experiments allow us to draw concerning the fixation-period of the number of rays in the fins, we have, however, succeeded in achieving one valuable result, viz. that the number of fin rays are chiefly fixed considerably before the stages in which the fin rays or their bases only begin to be visible.

VI. Abnormalities in the vertebral Column and the Significance of these Formations.

It is well known, that now and again abnormalities are to be found in the vertebrae and the processus spinosi in the vertebral column of fishes; everybody who has carried out racial investigations or has employed countings of the elements in the vertebral column of fishes in descriptions of species, will have met with various kinds of malformations in this part of the fish.

So much experience has been gained within this field, that the various kinds of abnormalities have been classified under names from similar formations in higher vertebrates. One of the most recent surveys has been given by Th. Schräder (1930), who has an extensive list of literature on the subject.

Most of these abnormalities are conspicuous and certainly often pathological deformities; various authors suppose, however, that some of them at any rate are congenital. Some of them are obviously caused by such special environmental factors as a species of fish may be subject to, when it approaches the limits of its existence, e. g. in water with a deficit of oxygen (Willer 1928) or when accumulation of certain substances — poisonous or otherwise unfavourable to the species — takes place; this may particularly happen in the case of species living in small rivers and lakes, but it may be found even in the case of oceanic species. Thus I have (1918, p. 35) mentioned features of this character in the oceanic fish *Myctophum glaciale* from the Sea of Marmara; here I found in individuals of this species, in contrast with what is true for specimens of this species from the open Mediterranean or from the Atlantic ocean, numerous examples of abnormalities in the spinal column. I observed that abnormally short vertebrae may occur among the normal ones, or the spinal column may be curved sideways in one or two places, or upward and down. In these cases undoubtedly we have to do with a phenotypic (pathologic?) phenomenon. But there are other abnormalities in the vertebral column connected with the vertebrae or/and the arches, which evidently do not belong to this category, but must be regarded from quite a different point of view. Knowledge of these abnormalities has been obtained during the minute racial investigations carried out during the last 30 years by fishery biologists and geneticists.

Schmidt (1921) was the first to discover and describe this formation in the Sea-trout, and he endeavoured through experiments to show its value as a link in the chain of vertebrae. Ford & Bull (1926), Ford (1933) and Ford (1937) mention the formation in the Herring, and Kändler (1932 and 1935) contributes highly to the understanding of these vertebral formations ("complex vertebrae" *partim*) and points out several interesting examples.

As these formations have not been coordinated with the well known abnormalities in the more recent surveys of abnormalities in the vertebral column, I shall here try to catalogue them systematically.

I give therefore below a summary of the various abnormal structures in the vertebral column of Teleosts, which may be of interest for the present investigation (see moreover e. g. Freund 1907, Schräder 1930 etc.).

I. Shortening and perhaps fusion of two or more of the centra, situated more or less irregularly along the vertebral column[1]).

1. Vertebral compression: the individual vertebrae are shorter, perhaps broader than the others, but they have not fused together.
2. Vertebral synostosis: the individual, shorter centra have fused together.

[1]) Ford and Bull (1926) have shown, that these formations — e. g. in the Herring — are generally found in the part of the vertebral column over the ventral fins and the anus.

II. Shortening and fusion of two (rarely more than two) of the centra in the vertebral column always situated at quite definite places in the vertebral column.
   1. Pre-urostyle vertebral synostosis: more or less pronounced fusion of two (very rarely more than two) centra in the vertebral column, situated immediately anterior to or partly belonging to the posterior uptilted portion of the vertebral column (sometimes visible only by a doubling of the ventral and probably also the dorsal arch).
   2. Post-cranial vertebral synostosis: vertebral fusion in connection with the first centrum of the vertebral column.

III. Spinal curvatures.
   1. Cyphosis: hump-back formation.
   2. Lordosis: hollow-back formation.
   3. Scoliosis: the vertebral column curved sidewise.
   4. Combination of hump- and hollow-back formation (Cypholordosis) or of hump together with a sidewise curvation of the vertebral column (Cyphoscoliosis).
   5. Plecospondyly: undulating row of curvatures in the vertebral column (particularly pronounced in e. g. Eels).

IV. Twin formations etc.

The pre-urostyle vertebral synostosis is of special interest to us and we shall refer to this formation more fully later on. I shall first, however, mention the post-cranial vertebral synostosis, which KÄNDLER deals with together with the pre-urostyle synostosis under the name of "complex vertebrae". I consider it necessary to distinguish between these two formations. The post-cranial vertebral synostosis which occurs in connection with the first, sometimes elongated vertebra — and which now and then has been found in e. g. *Pleuronectes platessa* (KÄNDLER 1932), and always (?) in e. g. *Salmo trutta trutta* — must without doubt be regarded from a point of view different from the pre-urostyle synostosis, because the extra spinal process (perhaps with neural arch) probably does not always belong to a centrum, fused together with the first vertebra, but in certain cases must be considered as belonging to the element, which has been included in the cranium (the basioccipital), and which constitutes the jointing with the first vertebra. I shall, however, not go further into the question about this formation, as it is of minor importance in relation to the present investigation.

When counting the vertebrae in the vertebral column of Trout fry there can rarely be any doubt how to number the vertebrae in the case of an ordinary vertebral synostosis or that of curvatures of the vertebral column; moreover, these malformations are of rare occurrence. In the case of pre-urostyle vertebral synostosis the matter is quite different; first of all because doubt often arises, as to whether the formation ought to be considered as 1 or 2 vertebrae, and then because these cases are of much importance when racial investigations are to be carried out accurately, as in certain samples they may appear in rather large numbers.

SCHMIDT (1921) is of the opinion, that in the case of the Sea-trout (*Salmo trutta trutta*) it is probable, that fused vertebrae have a value of 1.5 vertebrae, and he points out, that "fractions of vertebrae can actually be realized — in other words that also the personal values can be broken numbers — . ." SCHMIDT gives (l. c. p. 3) a sketch, which shows both a normal vertebral column of a young Trout and a vertebral column with fused vertebrae. FORD (1933) shows that the value mentioned (1.5) probably holds good also in the case of the Herring. The necessity of taking into consideration these formations in racial investigations is emphatically emphasized by KÄNDLER (1932 and 1935); particularly interesting is the fact, that "complex vertebrae" are to be found in almost half of the individuals in samples of Plaice from the

Baltic; various figures elucidate the conditions in the case of *Pleuronectes platessa, Pl. limanda, Pl. flesus* and *Clupea harengus* (KÄNDLER 1932); the formation has moreover been found in *Rhombus maximus*. SCHMIDT (1930) mentions the formation in *Gadus callarias*, and FORD (1937 p. 23) gives a list of no less than 37 species in which this formation ("complex segments") has been found, pointing out, however, that the formation is rare in *Percomorphi* and *Scleroparei*. And I may add, that the pre-urostyle vertebral synostosis has been found in almost all the species of fish the vertebral column of which I have had the opportunity to investigate, coastal fishes as well as oceanic fishes; e. g. also in the following species, which have not been mentioned by FORD (1937): *Sebastes marinus, Sebastes viviparus, Cottus scorpius* and various oceanic deep sea fishes particularly of the family *Myctophidae*. I expect that the formation will be found in practically all Teleosts, presumably, however, with a very low percentage among fishes in the tropics.

The situation of the formation immediately anterior to or near the place at which the notochord begins to bend upwards presumably partly holds the key to the understanding of its significance. I expect it is to some extent determined by the number of cells originally available for this part of the vertebral column and moreover by the space at disposal during the upbending of the notochord. Undoubtedly it should not be considered a pathological abnormality, but more likely a mechanism or regulator necessary to the organism in the cases when a higher or lower number of vertebrae (perhaps a fraction of a vertebra) owing to some external influence has been induced during the embryonal formation of the mesoderm segments and now has to be realized through the ossification of the centra. In the Sea-trout this segment, the preceding and the following two segments are the last segments in the vertebral column to ossify. The greatly varying percentage of pre-urostyle fusions of vertebrae within the various populations of a fish, as e. g. the Plaice[1]), seems to show that the formation is a regulating mechanism for the species.

These considerations lead to a question very important for our continued work concerning the influence of the environment on the number of vertebrae and particularly important to the theoretic explanation of the matter, viz. whether it is possible experimentally to produce or influence this formation. I shall therefore give some facts concerning this question, which, however, has not yet been finally settled.

First of all I shall briefly point out the main feature of the appearance and variation of the pre-urostyle vertebral synostosis in Trout calling attention to fig. 18 of the caudal end of a few selected specimens, which are offspring of H × G.

As previously emphasized, the irregularity nearly always appears in connection with the last but four vertebral segment (5th), only a few fusions having been observed in connection with the last but five (6th) or the last but six (7th) segment and never with the last but three vertebra (4th) in offspring of H × G. The appearance of the last four centra is nearly always the same from individual to individual, and it may be noticed, that during the ossification the last two centra early reach their normal height, while the antepenultimate centrum (3rd) and the last but three (4th) always ossify later in their dorsal part; sometimes the 3rd centrum, sometimes (usually I think) the 4th is farthest behind in development. The last but four centrum (5th) is very often broader than the 4th as well as the 6th; this may be observed most distinctly in the early stages, when ossification is not yet complete (i. e., before all the vitellum has been absorbed), but even when the ossification is complete, it may appear distinctly in otherwise quite normal vertebral columns; in early stages it is often observed, that

[1]) Showing e. g. 48 % in the Baltic, 8 % only in the open sea at Iceland.

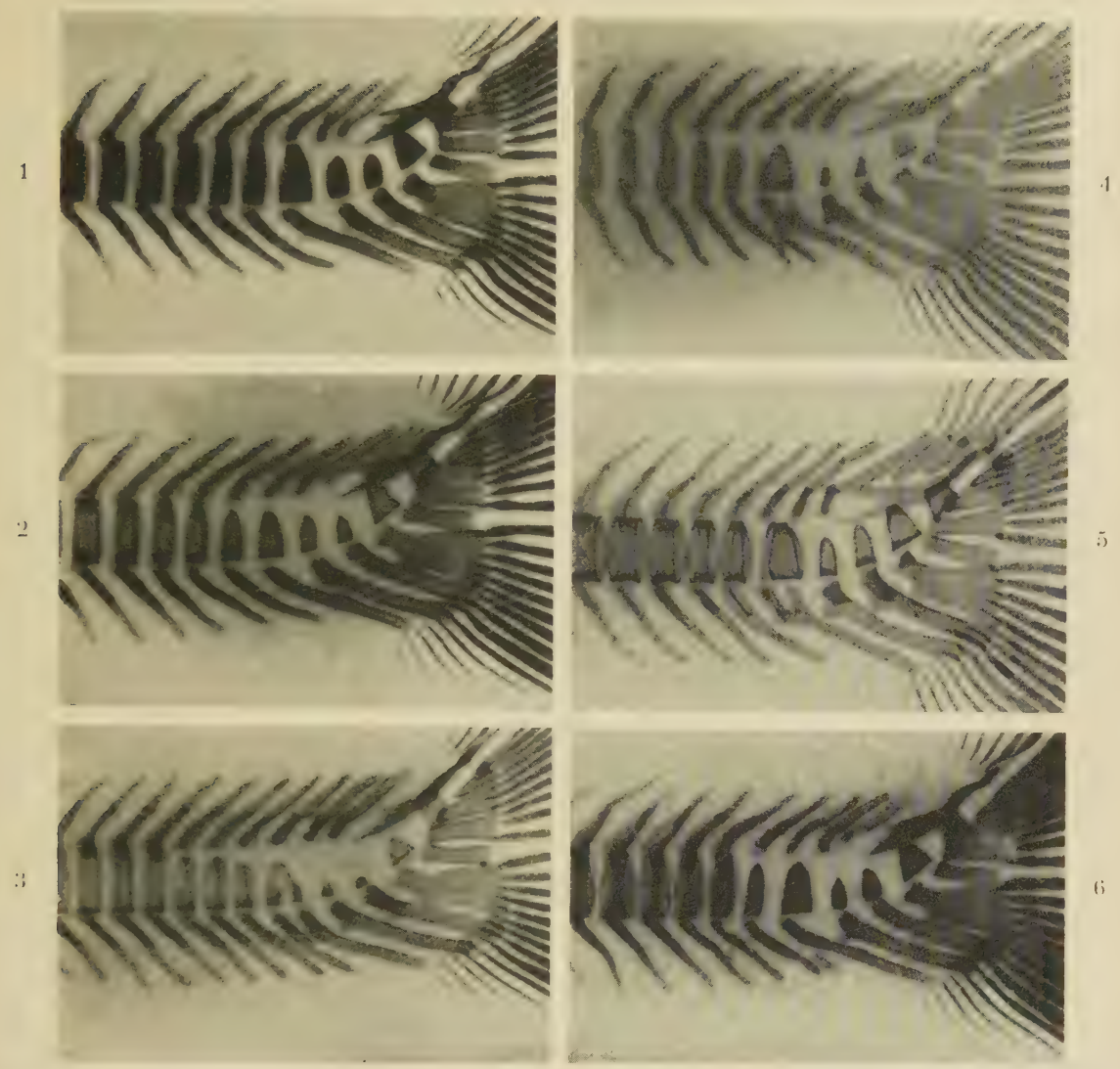

Fig. 18. Tip of tails of Sea-trout showing different categories of fusions. Photo: E. Bertelsen. **1:** normal distribution of epaxial and hypaxial elements, 5th vertebral segment, however, broader than normally; **2:** epural to 3rd and 4th vertebrae bifurcate; **3:** 5th vertebra double ventrally, with two hypaxial elements; **4:** 5th vertebra double with two epaxial elements and two partly fused hypaxial elements; epural to 3rd and 4th vertebrae bifurcate; **5:** 5th vertebra particularly broad; hypural bifurcate; **6:** 5th vertebra broad; a small extra hypaxial element anterior to the normal hypural.

the centrum is composed of two elements, the ossification proceeding from two ventral areas, which later on more or less fuse together apparently without leaving any trace of suture (cf. fig. 18, 3). Even if the centrum of the 5th vertebral segment is broader than the one anterior and posterior to it, I have not counted it as two, if the hypaxial elements have not shown that we evidently have a double formation. The cause of this is due to the fact, that the 5th centrum may be found in all stages from normal breadth to double breadth, and to count e. g. the broadest as two would be to introduce a mere estimation. Accordingly the appearance of the epaxial and hypaxial elements, in particular that of the hypaxial elements, is of paramount importance in our procedure of counting.

The number of arches connected with the last 5 centra is normally as follows: Of hypaxial elements[1]) there are 9 distributed in the following way:

1) to the terminal	vertebral segment	are	connected	4	elements[2])
2) - - penultimate	—	—	-	—	2	—
3) - - antepenultimate	—	—	-	—	1	—
4) - - last but three	—	—	-	—	1	—
5) - - - - four	—	—	-	—	1	—

While the posterior 8 elements nearly always exist and are very uniformly developed from specimens to specimens, with the greatest variation in the elements to the antepenultimate and the 4th centra, a double formation is, however, very often to be found in the hypaxial element to the 5th vertebral segment, but nearly always when this vertebral segment is of the broad type or is distinctly composed of two centra.

Of epaxial elements connected with the last 5 vertebrae there are most often and as the "normal" 5, of which the two posterior are situated above the peculiar bony sheath, which encloses the tip of the spinal cord and is evidently composed of 3—4 ossifications on each side; some scientists consider this formation as being transformed neural arches to the last centra. The number of epaxial elements connected with the last 5 vertebrae are now most often the following:

1) to the terminal	vertebral segment	1	dorsal caudal radial above the bony sheath mentioned.	[3])
2) - - penultimate	—	—	1 dorsal caudal radial above the bony sheath mentioned.	[3])
3) - - antepenultimate	—	—	1 epural, the base of which has usually been displaced forward, as if there was not room enough owing to the anterior bifurcate part of the bony sheath mentioned.	[4])
4) - - last but three	—	—	1 neural arch (+ neural spine) which also may be displaced somewhat forward.	[4])
5) - - last but four	—	—	1 neural arch (+ neural spine).	

Provided now that the 5th centrum is broad, a displacement of the epaxial element of the 4th segment may be so great, that it is impossible to decide whether this element belongs to the extra centrum, which has been included in the 5th vertebral segment, or is the epaxial element of the 4th centrum. Very often this phenomenon is accompanied by the fact that the antepenultimate epural shows a distinct bifurcation in its basal part or a division of another nature, which shows that the element is of a double nature, and therefore actually constitutes the fused elements of both the antepenultimate and the 4th vertebral segment (cf. fig. 18 (2, 4, 5)). I shall, however, not go further into a description of the different variations of these

[1]) Concerning terminology see R. H. Whitehouse, Proc. Zool. Soc., London 1910, p. 592.

[2]) The two posterior elements of these four are, however, small and not directly connected with the last vertebral segment.

[3]) In rare cases (and not in the offspring of the pair H×G) the terminal and penultimate vertebral segments may have only one dorsal radial.

[4]) In certain cases there may be found only one epaxial element to the antepenultimate and the 4th vertebral segment.

epaxial elements, as they have been used only subsidiarily in deciding whether the 5th vertebra ought to be counted as 1 or 2.

By the determination of the nature of the 5th vertebral segment, I have accordingly always — as had also in the main SCHMIDT 1921 — used the feature of the hypurals. Provided this element or the centrum itself is of a distinctly double nature the 5th vertebral segment is considered composed of 2 vertebrae and is accordingly counted as 2. The double formation may most often belong to one of the following four groups: **1**) two separate hypaxial elements of the same or almost the same size (cf. fig. 18, 3), **2**) a distinct hypural with an extra small element most often situated anterior to the normal element, thus a rudimental free *processus spinosi* (cf. fig. 18, 6), **3**) a bifurcation of the basal part of the element, viz. the neural arch (cf. fig. 18, 5), **4**) both a bifurcation of the basis and an extra free or fused smaller element (cf. fig. 18, 4).

In order to avoid mistakes concerning the judgement of the pre-urostyle synostoses, it is as we said, necessary to preserve the fry for counting at a practically uniform stage of development; by this procedure we can exclude uncertainty owing to changes in the extent of ossification as the individuals grow older. I have therefore, as said, practically always preserved the material after about 800 D°, so that a fairly uniform material has been at my disposal.

S..... Total no. of vert.	51—52	52—53	53—54	54—55	55—56	56—57	a. 5.+6.	b. 6.—8.	Total no. of specimens
61	..	..	..	..	..	1	1	..	3
60	..	..	..	..	29	..	29	..	66
59[1])	..	1	1	242	..	..	242	2	1341
58	2	..	13	..	..	..	13	2	921
57	..	..	..	..	..	..	..	..	3
Total...	2	1	14	242	29	1	285	4	2334[2])

S = serial numbers of the fused vertebrae.
a = 5th and 6th ultimate vertebrae fused.
b = fusions of other numbers of vertebrae.

[1]) + 1 with the vertebrae nos. 19th and 20th fused.
[2]) Average number of vertebrae:
1) 5. + 6. counted as 2: $a_{2334} = 58.63$
2) 5. + 6. — - 1: — = 58.51
3) 5. + 6. — - 1.5: — = 58.575
4) exclusion of all pre-urostyle synostoses:
$a_{2049} = 58.574$.

In the above table a survey has been given of the number of all fusions observed in the examined 2334 specimens being offspring of H × G. Out of this material the 5th vertebral element in 285 individuals — i. e. in 12.2 % — has its origin in the last but four (5th) and the last but five (6th) vertebrae according to our definition. Among the large quantity of material fusions have moreover only been observed in 5 cases in other places of the vertebral column.

We shall then return to the important question: Is it possible to produce pre-urostyle fusions experimentally? Primarily it is necessary to investigate, whether the actual number of fusions in samples developed at various temperatures is different, and then

whether the number may be influenced, provided the samples are transferred from one temperature to another at some moment during their development.

In the following survey the percentage of fusions in progeny of the two Trout H and G has been indicated; the fry of this pair is the material best fitted for this investigation (see moreover p. 9 et seq. and p. 21 et seq., where information is to be found as to the conditions during the development of the offspring of this pair, as to the transfers carried out etc.).

It may now be observed from the table below, that the control samples show the highest number of fusions at the lowest temperature (18), fewest at the highest and intermediate temperature (7—14), showing, however,. much variation at the intermediate temperature. The results from the pairs of Trout A×C and B×D show the same feature; those from the pair E×F, however, approximately equal numbers of fusions.

Percentage of fusions in offspring of H×G:

	Control sample at the initial temperature				Control sample at the terminal temperature
A:	3°	3° →	6°		6°
		142 D°	215 D°	358 D°	
%	**18**	**11**	**9**	**16**	**7**
B:	6°	6° →	3°		3°
		168 D°	275 D°	466 D°	
%	**7**	**15**	**19**	**18**	**18**
C:	9°	9° →	6°		6°
		191 D°	299 D°	425 D°	
%	**9**	**13**	**9**	**9**	**14**
D:	6°	6° →	9°		9°
		155 D°	242 D°	442 D°	
%	**14**	**13**	**10**	**8**	**9**

In one of the series above a distinct displacement of the percentage of fusions is evident after the transfers, viz. in the series B, where the samples from all the transfers from 6° to 3° show a considerably higher number of fusions than the initial sample. Moreover it may be observed, that in the series A (3°) the two earliest transferred samples have got nearly the number which is found in the control sample in the series to which the transfer took place. In the other series there are less conspicuous changes, or the changes are quite irregular. As we have seen (p. 30), that changes in the meristic characters may possibly depend on whether the influencing temperatures are lower or higher, it is probable that the fact pointed out here is of real importance, the most distinct changes being found only at the low temperatures.

In the series employed here, the total number of fusions might produce only a slight change of the average number of vertebrae, most often only 0.10—0.15 vertebrae, if the fusions are counted as one instead of two (cf. note [2]) to the table p. 37); we cannot therefore expect

to settle the question, whether the fusions may be subject to influences of the temperatures through investigations of the variation of the vertebral averages alone.

We have, however, a result from another of the series (E × F) which seems worth mentioning in connection with the problem of external influence on the fusions. Primarily it must be observed, that the mortality among eggs from the pair E × F was rather considerable, as was also the mortality among fry in the sensitive stage just after hatching (a total of about 41 % eggs and fry died, of this 28.9 % eggs). The hatching took place under exactly the same conditions as for the series H × G, but in this series as mentioned only 0.4 % eggs and 2.4 % fry died, a total of 2.8 % only. The cause of the mortality is, however, quite obvious, the female (E) one night before it was used in the experiments, jumped out of the basin and was found dead in the morning on the cement floor; on opening the dead and stiff female the eggs were found quite ripe and in good condition, and therefore artificial fertilisation was carried out and appeared far from unsuccessful.

The fully developed offspring shew, however, several abnormalities in the vertebral column (fusions, twins etc.), and had often fused hypural elements etc., but as the majority was well developed and easily countable with a fairly normal number of pre-urostyle fusions (12—16 %), I have employed the series in various ways. It is interesting to notice, that the numerous abnormalities doubtless are due to the fact that the eggs have been subjected to influence previous to their fertilisation. And the influence has either been a mechanical one, viz. the violent shakings to which they had been subjected, as when the fish had been lying and jumping on a cement floor during a fairly long period until it died, or, the influence on the eggs has been of a chemical nature through their lying for some hours in the abdominal cavity of the dead fish.

A batch of the eggs, which was incubated at 3°, was transferred some time after reaching the "eyed-egg" stage (viz. at 279 D°) to 9°, at which temperature they went through the remaining stages of their development. The number of pre-urostyle fusions was in this transferred sample double the number which normally was to be found in individuals incubated at 3°, and it was the haemal arch to the last but four vertebral segment which more than normally had become a double formation. The conditions will be seen in the following table, which gives the number of fusions in 100 individuals examined.

	Sample developed at 3°	Sample transferred from 3° to 9° at 279 D°	Sample developed at 9°
2 separate haemal arches to the fused last but four and last but five vertebrae	8[1])	7	3
1 haemal arch to these vertebrae consisting of two fused elements	3	17	13
Total	11	24	16

It is evident that a change has taken place here through the transfer from 3° to 9° regarding the haemal arch belonging to the elongated 5th vertebral segment in some individuals; the appearance of the haemal arches shows distinctly, that they are composed of two elements.

[1]) Also one specimen with double haemal arch to the fused 7th and 8th vertebrae counted from the tip of the tail.

Even though this sample of the pair E × F has a special position in relation to H × G-individuals — owing to the life history of the mother fish — it is worth noticing, that here the visible signs of typical pre-urostyle synostosis have been produced experimentally through a change of the temperature; the double nature must therefore be present in a latent condition in the last but four vertebral segment much more often than has been recognized; and this is supported by the fact, that this segment is often longer than both the segment anterior to and that posterior to it, without other evidence of its double nature.

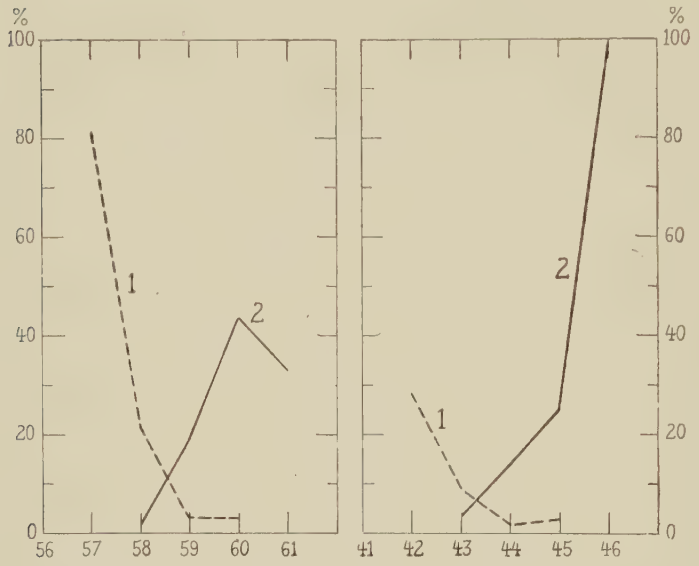

Fig. 19. Percentage distribution of pre-urostyle fusions in each class of vertebrae. 1: the fusions counted as 1 vertebra, 2: the fusions counted as 2 vertebrae. To the left: in Sea-trout (*Salmo trutta trutta*), 2334 individuals of the 0-group with 12.2 % fusions; to the right: in Plaice (*Pleuronectes platessa*), 1843 individuals of the 0-group from Iceland with 8.4 % fusions.

We shall in this connection refer to the conditions mentioned in footnote[1]) p. 27 as they also indicate that the pre-urostyle synostosis is, if not produced by, yet strongly influenced by the temperature.

In the present work the pre-urostyle fusions as mentioned are counted as 2 vertebrae according to the definition, that the haemal arch shall be of double nature, if the vertebrae are to be regarded as two. Schmidt (1921) has shown, that the value presumably is about 1.5.

Kändler (1932 and 1935) points out that the fusions in the case of the Plaice are most numerous in individuals with a low number of vertebrae. This, however, is due to the fact that the fusions are counted as 1; if they are counted as 2, we get the reverse result, viz. that the fusions will be most numerous in individuals with a high number of vertebrae. In figure 19 I have given as an example the percentage of fusions belonging to the various numbers of vertebrae in the case of two kinds of fish, viz. in Plaice from Iceland (of which about 1800 countings of 0-group individuals have been carried out) and in the Sea-trout from Denmark (of which 2334 countings from offspring of the pair H × G have been used). The continuous curve shows the pre-urostyle fusions counted as 2 vertebrae, the other curve (dotted) counted as 1 vertebra. I find the first method of counting most practical; but the number of fusions ought to be indicated, as e. g. here in the tables p. 52 et seq.

VII. The experimental Results compared with certain so-called racial Differences in some marine Fishes.

In 1931 Schnakenbeck very sharply opposed the tendency of fishery investigations to consider, during recent years, certain meristic characters as more or less unstable, though they hitherto had been treated as reliable, racial characters, genetically determined. The

new view was supported particularly by SCHMIDT's racial investigations and experiments concerning racial characters. In the work mentioned SCHNAKENBECK frequently expresses his opinion, which in particular is supported by the appearance of the percentage frequency curves based preferably on vertebral countings of Herring. In an extensive preface he attempts to reduce a series of results achieved by various researchers into the lability of certain meristic characters to be only indications of lability or on the contrary simply proofs of his own view (cf. l. c. p. 434—455, where works by SCHMIDT, JOHANSEN, HUBBS, LEA, BJERKAN and TÅNING are criticised). SCHNAKENBECK's view met with opposition from the biological as well as from the statistical side[1]), and during the following years a number of works were issued, based on racial investigations into various species of marine fishes, and dealing with the possibilities of modification of certain meristic characters. These works have, however, favoured the view among the fish investigators that a certain lability is present, and has moreover contributed in creating distrust as to the value of subtle meristic racial differences — between e. g. certain Herring races. This was very clearly expressed at the international meeting concerning Herring investigations at Lowestoft 1935 (see Rapp. et Procès-Verbaux des Réunions, Vol. 100, p. 7—9 and moreover e. g. DAVIS' contribution p. 12—13). The greatest scepticism as to the usefulness of the number of vertebrae in racial studies seems, however, to have been shown by KÄNDLER (1935, p. 472).

The general view of these questions has on the whole been contrary to the view which SCHNAKENBECK favoured, but which he himself, however, evidently has modified a little since 1931 (see Rapp. et Procès-Verbaux, Vol. 100, p. 28 et seq.). Unfortunately the experimental race research work upon fishes has not been able, so far, to give a clear and unmistakable proof concerning this matter. The reason for this is, that not until the years just previous to the war has it been possible, without too high a percentage of loss, successfully to rear the fry of salt water fish to such advanced stages, that the number of vertebrae, fin rays etc. might be exactly determined (cf. G. ROLLEFSEN's experiments on Plaice and Flounders mentioned in "Naturen", Bergen, 1940, pp. 197—217).

As the experiments on fry of Sea-trout, which is dealt with in this small paper may throw some light also on these questions, I propose to consider them briefly here.

Perhaps the difference in the average number of vertebrae which has been obtained through the present experiments with Trout developed for instance at the two temperatures 3° and 6°, namely about 0.5 vertebra, may be considered very slight. I shall therefore for comparison give some curves from investigations into another species of fish, the Herring, which show, that such a difference in the average number of vertebrae has been attributed a considerable value when distinguishing between races in nature.

Results concerning the Herring have been selected for the present purpose partly because suitable material of this species is available, and partly because the Herring has a similar number of vertebrae as the Sea-trout and shows a similar range of variation.

In fig. 20 I have reproduced a figure from W. SCHNAKENBECK (1931, fig. 8, p. 467) which shows the percentage distribution of vertebrae in a series of Herring samples from the North Sea, namely from the waters between the Channel and the Fladenground. The average numbers of vertebrae of the 9 curves is situated between 56.36 and 56.77, thus with a difference of 0.41. SCHNAKENBECK is of the opinion, that the samples represent two Herring races, viz. the Bank-herring and the Channel-herring and he says about the figure (l. c. p. 467):

[1]) See e. g. SVEN RUNNSTRÖM (1933) and BUCHANAN-WOLLASTON (1933).

"Die beiden unteren Kurven zeigen den gleichmässigen Variabilitätsmodus des Merkmals Vert. S. für den Bankhering, die beiden oberen den für den Kanalhering. Die dazwischen liegenden Proben bilden Mischungen aus beiden Rassen, wobei der Anteil der einen oder anderen Rasse jeweils ganz verschieden stark ist". Samples of these two Herring races have later on in the same paper been discussed more elaborately by Schnakenbeck and results obtained during the course of several years have been shown (p. 478—79) in order to ascertain the constancy of these two races.

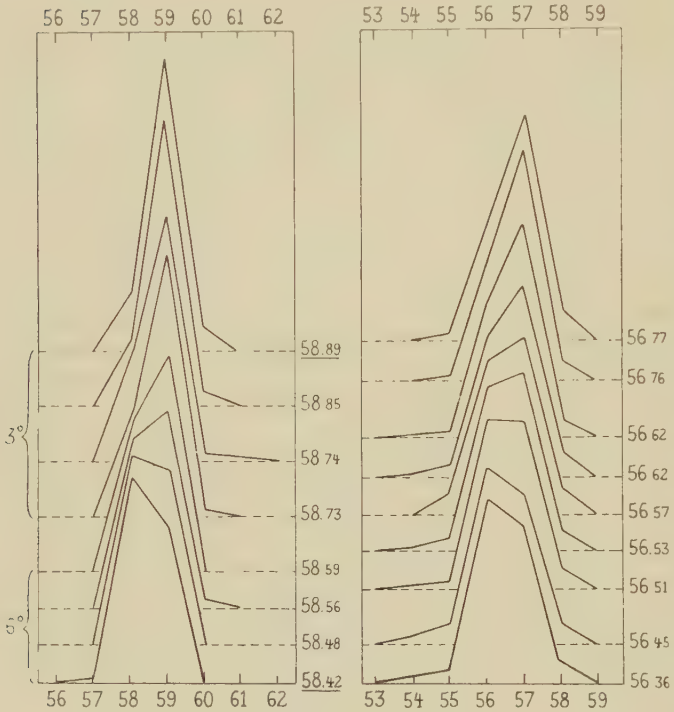

Fig. 20. Percentage frequency polygons of vertebral countings of Trout samples to the left and of Herring samples to the right. The Trout samples: all being progeny of the same parents (H × G), but incubated at 3° or 6°. The vertebral averages to the right; the underlined figures: the controls; not underlined figures: transferred samples. The Herring samples: the uppermost polygons represent Channel-herring; the bottom polygons Bank-herring; the intermediate polygons are considered to represent mixed samples of these two races. Right fig. from Schnakenbeck 1931. Cf. the text.

I have now for comparison arranged (in a similar way as in Schnakenbeck's figure 8) percentage curves of the number of vertebrae obtained through the hatching experiments with Sea-trout at two temperatures, viz. 3° and 6°; 4 samples from each series being used. The eggs have been kept at 3° and 6° respectively, until the fixation-period of the number of vertebrae evidently had been passed (about 140—190 D°). The curves are as in Schnakenbeck's figure arranged with the lowest number (58.42) below and the highest number (58.89) at the top. The difference between these two extremes is 0.47 as in the samples of Herring shown in fig. 20 to the right.

It will now be seen, that there is practically no visible difference between the two figures. But there is the very important difference, that while Schnakenbeck considered the Herring samples as representing two well defined races of Herring, we know that all the samples of Sea-trout are offspring of the same parents, the eggs of which have been kept at 3° and 6° respectively until the fixation-period of the number of vertebrae had in the main been passed. The comparatively slight difference in temperature of 3°, to which eggs of Trout easily could be exposed in nature, has thus been sufficient to give the percentage frequency curves of the number of vertebrae the same appearance as those of the Herring. Moreover the average numbers of vertebrae show the same difference which, in the case of the Herring, has been emphasized as one of the proofs that the samples represent two well-defined Herring races. This of course does not involve, that the two groups of Herring are not genetically different; but it is obvious, that the proof of this must preferably be founded on a base other than the number of vertebrae. Provided the fixation of the racial characters takes place also in Herring at such an early stage as the present experiments seem to indicate for Teleosts generally, and provided the Herring like certain other marine

animals only will or can spawn inside a certain narrow interval of temperatures, an obvious constancy of the characters, particularly of the number of vertebrae, might be expected.

Fig. 21, which gives the results from another series of hatchings of eggs of the same pair of Trout, but at the temperatures 9° and 6°, shows on the whole the same as fig. 20, but with still greater difference between the extreme samples and therefore somewhat different from SCHNAKENBECK's figure, which I have chosen here for comparison. All details as to the various samples employed in the two figures (20 and 21) are to be found on p. 25 et seq. and in the tables.

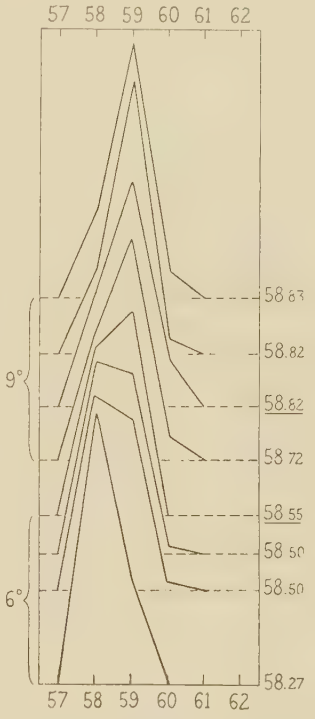

Fig. 21. Frequency polygons of vertebral countings of progeny of Sea-trout (H × G), incubated at 9° or 6°; cf. the preceding figure.

Besides the Herring example from the North Sea just mentioned, various others in the literature might be referred to; but here I shall mention only one other example, which I published some years ago (1929), namely the variation of the number of vertebrae in Plaice at Iceland; this variation I regarded as a phenotypic phenomenon. SCHNAKENBECK (1931) found it evidently difficult to interpret this example as genotypically and not phenotypically determined; his interpretations find no support, however, in the life history of the species at Iceland (migrations, spawning places etc.); and I shall here not discuss his view, that the Icelandic stock of Plaice consists of two races, nor disprove various mistakes in his account of conditions in Icelandic waters, as it can hardly any more be of interest. But I shall confine myself to giving a series of curves (fig. 22) derived from more recent countings of Plaice from Iceland. These countings have been carried out exclusively on 0-group Plaice, of which about 1800 specimens have been employed from a number of localities situated all round Iceland; by means of this material probable errors are avoided which might be connected with the former material, because this was composed of both 0-group individuals and individuals several years old. By comparison with my figures from 1929 it will be seen, however, that the difference between this earlier material and the present material is in the main without any importance.

Now I have here in fig. 22 arranged the curves — which are percentage curves like those in the preceding Herring example — in such a way, that they start from the warmest part of the long coastal line of Iceland (at Portland) and from here follow the coast in a clockwise direction to the north coast and the south-east corner of Iceland, i. e. to the coldest part of the island. On the whole a continuous increase of the averages will be seen until North-Iceland has been reached, while no pronounced change takes place from here and round to East-Iceland. It must be assumed that provided we had a sample from the territory between Portland on the south coast and South-east Iceland, this would constitute a distinct transition stage between the curves denoted "Ho" and "Po" in fig. 22. The increase from the warm to the cold water is about 0.5 vertebra, and it may undoubtedly be quite correct to consider the example as an experiment carried out by nature itself, because the fall of the temperature round Iceland corresponds to the temperatures, which might be established in a series thermostat. The current round Iceland (which is anticyclonic) has, however, of course carried eggs and fry far away from the actual spawning places, which are chiefly situated along the south and west coast of the island.

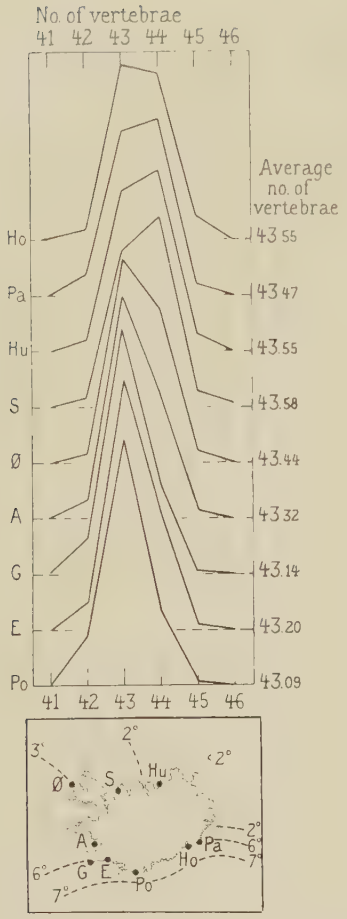

Fig. 22. Frequency polygons of countings of vertebrae of samples of Plaice fished in coastal waters round Iceland. The letters on the small chart and to the left of the frequency polygons correspond. - - - - - the isotherms in 50 metres of depth in the spawning period of the Plaice. See the text p. 43.

The change of the number of vertebrae, viz. about 0.5 vertebra, corresponds entirely with that produced by a difference of temperature of about 3° in case of Trout fry. The difference in temperature to which the spawning Plaice are exposed in Icelandic waters is presumably of a similar size, viz. about 4°.

As my aquarium experiments with Plaice have been unsuccessful owing, *inter alia*, to present difficulties in producing suitable food (*Artemia*) in sufficient quantities, I can for the time being give only the curves derived from Plaice caught off Iceland, hoping that some day circumstances will make it possible to produce a similar series of curves from laboratory experiments.

VIII. Survey and concluding Remarks.

In a paper from 1921 Schmidt has shown, that the number of vertebrae in the case of the Sea-trout depends on the temperature in a definite and peculiar way — the highest number is produced experimentally at both low and high temperatures, while the lowest number is produced at intermediate temperatures about 6—7° C.; and during the last few years this result has been confirmed as shown in this paper by several new experiments with Sea-trout. Moreover experiments with Sea-trout carried out during the last years at various temperatures (viz. 3°, 6° and 9°) have shown, that the number of rays in the dorsal and pectoral fins increases with rising temperatures, while the average number of the anal fin rays shows only a slight difference at the various temperatures, though with a minor fall at the highest experimental temperature, viz. 9°. By comparing these results with those achieved by means of investigation of various fishes in their natural surroundings, contradictory as well as confirmatory results may be found, and only through continuous experiments with Trout and other fishes, there may be any hope of finding the general laws, which may be supposed to apply with regard to the fixation of the numerical values.

Moreover the results of the experiments described above, based on transfers of Trout eggs from one temperature to another, have shown that the embryo is not susceptible of a decisive change of the average number of vertebrae if it is more than 150 D° old, which equals about 17 days at 9°, about 25 days at 6° and about 50 days at 3°[1]).

In this stage the embryo is still very young as shown in fig. 3, p. 8; it is for instance rather uncertain, whether the last developed mesoderm segments in the tip of the tail can be counted with certainty. Whether the fixation of the number of vertebrae takes place much earlier I do

[1]) The number of days from fertilisation until hatching of the first egg is at these temperatures about 43, 68 and 117 days respectively.

not know, as the experiments concerning this problem have not yet been finished. But it must be supposed, that if it is determined at such an early stage in the development as shown, the moment will presumably be situated about the days or perhaps the hours, when the cell groups of the mesoderm segments in the tip of the tail have been separated. In case of our common salt water fishes such a stage will presumably always be previous to the hatching of the egg[1]), and it may therefore a priori be supposed, that the final number of vertebrae in all these fishes has been determined previous to the hatching of the egg.

The few experiments carried out so far concerning a determination of the fixation-period for the final number of rays in the dorsal, anal and pectoral fins in the Trout have promised that a solution of this question might be obtainable.

In certain cases, however, quite unexpected effects may be observed, showing that unknown factors have intervened; or the effects may be so small, that they are statistically insignificant.

In several cases, in which significant effects have been obtained, it is apparent, that a change may take place throughout a longer period; the fixation-period for the fin-rays is accordingly not of a short duration. As regards the fins investigated, the fixation-period for the number of rays seems to begin previous to or in the eyed-egg stage; for the anal fin it seems in the main to end about 300 D°, for the dorsal fin at about 400—500 D° and for the pectoral fin much later (probably at more than 1000 D°). But in the main the number of fin rays has been fixed considerably earlier than in the stages when the rays or the basal part of these begin to be visible, thus previous to hatching.

Between the dorsal and the pectoral fin a peculiar correlation has been observed with regard to the variation of the number of rays, though the mode of development is very different in these two fins (see fig. 17, p. 31).

It should be added, that a change of the average number of fin rays beyond 0.5—1 ray has not been observed under the present experimental conditions, neither in case of the dorsal and anal fin, nor in case of the pectoral fin.

It can hardly be expected a priori that the speed at which the various developmental processes takes place may be effected in the same way by a change of the temperature; some processes presumably may be advanced, others delayed; this has been mentioned by several authors (e. g. Gray (1929)). It is therefore scarcely due to mere chance that low temperatures seem to have quite other effects on certain characters in our animals than higher temperatures. It is, however, obvious, that far more extensive experiments than the present must be carried out in order to discover the general laws which govern the developmental processes considered.

The results achieved through transfers from one temperature to another show that a certain period of the embryonic development may be considered as an indifferent period with regard to the fixation of the meristic characters examined; this period may probably extend from the first cleavage stages until the moment during the embryonic development, when the meristic character in question has commenced to get the greater part of its elements formed, though not all. The period during which the formation of the remaining elements takes place may then properly be called the fixation-period. The period in which

[1]) In the majority of fishes the number of myotomes, specific of the species, is evidently developed in the embryo previous to hatching. But there are, however, exceptions to this rule, as e. g. several oceanic muraenoid fishes add numerous myotomes after the hatching, i. e. in the *Leptocephalus*-stage. Moreover anybody who has hatched fry of fishes in the tropics knows, that many fish larvae here leave the eggs at such an undeveloped stage, that the number of vertebrae can hardly be finally fixed.

the meristic characters are specially exposed to external influences, has been called the critical, sensitive or plastic period. After this period there should be no or only slight possibility of a change in the number of segments or rays. The limits of the fixation-period for the several meristic characters must be determined through further experiments[1]).

Various experiments with the object of rearing marine fishes to the developmental stage, at which the vertebrae may be stained and counted with certainty have as yet failed; but G. Rollefsen's successful experiments with fry of flat fish promise, that these experiments in the near future may produce very valuable knowledge as to the conditions also in the case of marine fishes. Rollefsen points out quite briefly and without referring to detailed experiments, that the number of vertebrae and fin rays seems to be determined by the temperature during the first 8—14 days after hatching; if this is really so, the conditions with regard to the fixation of the number of vertebrae are evidently different in various Teleosts. We must, however, look forward to the publication of the particulars, before we draw more far-reaching conclusions concerning this question.

There can be no doubt, that much would be gained for fishery investigations, if it turned out, that in the case of all our economically important species of fishes it was a general rule, that the number of vertebrae — thus, the racial character most generally used — was already fixed previous to the hatching. It would then be necessary in order to study the influence of the environment, e. g. in the case of the Herring, to investigate only the environmental characteristics for a fairly short period along the bottom of the sea, where the eggs are deposited. And for the Cod and other species with pelagic eggs it could be maintained, that for similar studies it would be sufficient to know the conditions in or near the surface of the water (apart from spawning grounds of a special nature, as for instance in the eastern Baltic). And in order to ascertain the influence of possibly effective factors, viz. temperature, salinity, oxygen etc., all species of fish should be investigated only in the comparatively short period immediately following the maximum spawning, while the much longer period passed as post-larva needs no investigation in that respect. It is accordingly very desirable, that the fixation-period for the number of vertebrae in our most important food fishes should be determined as soon as possible.

The results obtained through the present experiments like the very interesting results achieved by Mottley (1934, 1937) emphasize the justification of the scepticism which in the course of the last twenty years has arisen as to uncritical employment of certain subtle "racial characters". Some of the results mentioned here show that a variation of the number of vertebrae of the same size, which has been used to separate e. g. two Herring races in the North Sea, has easily been produced in offspring of the same parents of Trout if developed at only slightly different temperatures (e. g. 3° and 6°). This shows the necessity of carrying through the experiments on the commonly employed racial characters in fishes as extensively as possible. It will then perhaps be possible to get a reliable knowledge of what is genotypically and what phenotypically determined within the racial characters employed within each individual species.

Here the question arises: How great an effect on the average number of vertebrae will it be possible to produce experimentally? Will it be possible in certain species of fish experimentally to produce variations equal to those found in some species or racial groups in nature? As yet we have, however, very little or no knowledge of this important question.

[1]) C. McC. Mottley (1934 p. 10) points out, that the number of scales in *Salmo kamloops* is fixed in the stage following the eyed-egg stage; but the upper limit has not yet been determined.

The greatest difference in the average number of vertebrae in for instance the Plaice is found between the populations of the Baltic and Iceland with 42.20 and 43.58 as the lowest and highest average number of vertebrae, thus with a difference of 1.38 vertebrae; round Iceland proper we have found a variation of about 0.5 vertebra. Now it seems to be within the range of possibility to produce experimentally — by means of a change in the temperature, probably together with a change of one or several other environmental factors — an effect as considerable as that noticed in Plaice from Iceland and the Baltic respectively, and then to approach a decision whether this difference ought to be considered as being genotypically or phenotypically determined.

Considering the great difference in the number of vertebrae, which may be found between populations of certain other northern species of fish, e. g. *Ammodytes* (cf. Ad. S. Jensen 1941, 1944), we might easily suppose, that such a great variation cannot be phenotypically but must be genotypically determined. It is most likely that even minor variations in meristic characters may be genotypically determined in many cases, because it has been proved by Schmidt in the case of two of the subjects he has investigated, viz. the tropic fish *Lebistes* (1919) and the northern fish *Zoarces* (1920).

By carrying out experimental racial investigations we must so far take it for granted, that a difference between e. g. the number of vertebrae of two populations of fish may be partly genotypically, partly phenotypically determined, and only by experiments may we arrive at an "either . . . or" or "both . . . and". The object of the experimental racial investigations must primarily be to elucidate the extent of the modifications which is possible in response to certain environmental changes within the countable characters of the species of fish under consideration.

As an important link in the investigations carried out, certain abnormalities in the vertebral column, which are here named the pre-urostyle vertebral synostoses, were treated at some length pp. 32—40, and it is shown, that these formations seem liable to external influence. Presumably a certain mechanism is hidden in these fusions rendering a slight change in the average number of vertebrae possible, even though the vertebral column has been founded.

In the present paper the influence of temperature only has been treated; and this might easily leave the impression, that I consider temperature the only effective environmental factor. I will, however, point out, that this is not so, as we still practically know nothing of the power of other environmental factors to influence the meristic characters; future experimental work must include studies in the influence of factors like salt, oxygen, the space factor etc.

Surveys of results concerning racial investigations in fishes and of interpretations of the observations obtained have been given by several authors in recent times, among whom may be mentioned: Redeke (1912, 1915), Schmidt (1917), Schnakenbeck (1931), Hubbs (1934) and Vladykov (1934). I here beg to refer to these authors; but as already mentioned in the preface of this small paper, the results based on experiments have been very few, indeed recent authors constantly emphasize, that it is now indispensably necessary to include experiment in racial investigations to a far greater extent than has previously been done.

I shall not here recapitulate the various attempts to interpret the phenomena, but only briefly mention that Hubbs and Johnsen have endeavoured to find an explanation of the fact, why one or another of the meristic characters sometimes shows a lower sometimes a higher

average. Hubbs (1926 p. 75—76) says about this: "the addition of somites, which is practically synonymous with the growth of the embryo, proceeds faster under accelerating than under retarding conditions of development, but terminates relatively sooner and more abruptly. As a consequence, warm or brackish water forms of a species of fish have as a general rule fewer vertebrae than the forms inhabiting cooler or more saline water." And Johnsen (1934 p. 23) comes to the following conclusion in his interesting theoretical explanations, particularly based on Schmidt's experiments with Sea-trout: "The "total effect" (of the environmental factors) has hitherto been assumed to be the rate of the development of egg and larva; a short development has been correlated with a low number of vertebræ, a long development with a high number of vertebræ. More precisely, the total effect of the external factors may be defined as the length of the formative period, that is, the period during which a numerical character is established. The units of a numerical character are not, as a rule, established all at once but appear successively during development. This circumstance may explain why a short formative period is correlated with low values and a long formative period with high values of a character which, like the vertebræ, exhibits a variation in number."

It is, however, so far as I can see, too early to adopt this as a general rule. This seems to be particularly emphasized through Schmidt's results and my more recent repetitions of them regarding the influence of low, intermediate and high temperatures on the number of vertebrae in Trout, with the effect that low as well as high temperatures[1]) produced a high number of vertebrae; i. e. a very long as well as a very short "formative period" has in this instance caused the same result.

If I now publish the preceding few results of the experimental investigations without giving detailed comparisons with results from nature and without endeavouring to establish more general "rules", it is from the firm conviction, that this would be premature and of no use to anybody in the extensive experimental work which is in store concerning this species of fish, as well as many other species which ought to be included in the investigation. Up till now the few experiments carried out, have given rather unexpected results, so all theorising in my opinion ought to be postponed until more material makes it justifiable.

[1]) In spite of a uniform, rather high percentage of oxygen in my experiments (cf. Johnsen l. c., p. 16—18).

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[1]) * = papers with extensive lists of literature.

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X. Tables.

Table 1. Series A. **3°** (a—c: 3° → 6°). **H × G** 1943.

No. of vert.	Co. A No. 1	a: 142 D° No. 2 → 10	b: 215 D° No. 5 → 11	c: 358 D° No. 5 → 9	3° → 9° No. 1 → 17 213 D°
61	..	..	..	1	..
60	5(3)	1	3(1)	2(1)	5(3)
59	79(15)	71(11)	79(8)	67(15)[1]	74(11)[2]
58	16	28	18	30	21
57	..	..	..	..	..
n	100(18)	100(11)	100(9)	100(16)	100(14)
A	**58.89**	**58.73**	**58.85**	**58.74**	**58.84**
σ	±0.447	±0.469	±0.435	±0.544	±0.487
P. E. A.	±0.0301	±0.0316	±0.0293	±0.0367	±0.0328
P. F. A.	±0.15	±0.16	±0.15	±0.18	±0.16
No. of D-rays					
16	..	1	..	..	..
15	21	49	51	37	67
14	64	47	45	61	32
13	15	3	4	2	1
n	100	100	100	100	100
A	**14.06**	**14.48**	**14.47**	**14.35**	**14.66**
σ	±0.600	±0.577	±0.579	±0.522	±0.498
P. E. A.	±0.045	±0.0388	±0.0390	±0.0352	±0.0336
P. F. A.	±0.20	±0.19	±0.20	±0.18	±0.17
No. of A-rays					
14	..	..	2	..	2
13	56	40	46	62	55
12	43	60	52	37	43
11	1	..	..	1	..
10	..	..	..	..	..
n	100	100	100	100	100
A	**12.55**	**12.40**	**12.50**	**12.61**	**12.59**
σ	±0.523	±0.494	±0.545	±0.492	±0.536
P. E. A.	±0.0352	±0.0332	±0.0367	±0.0332	±0.0361
P. F. A.	±0.18	±0.17	±0.18	±0.17	±0.18
No. of P-rays					
14	..	8	9	4	3
13	64	86	87	90	87
12	36	6	4	6	10
n	100	100	100	100	100
A	**12.64**	**13.02**	**13.05**	**12.98**	**12.93**
σ	±0.484	±0.376	±0.360	±0.326	±0.356
P. E. A.	±0.0326	±0.0253	±0.0242	±0.0220	±0.0240
P. F. A.	±0.16	±0.13	±0.12	±0.11	±0.12

[1]) + 1 with 53rd and 54th vertebrae fused. [2]) + 1 with 52nd and 53rd vertebrae fused.

Table 2. Series B. **6°** (a—c: 6° → 3°). **H × G** 1943.

No. of vert.	Co. B No. 7	a: 168 D° No. 8 → 4	b: 275 D° No. 9 → 3	c: 466 D° No. 9 → 3	Co. B. No. 7. 6° p.[1]) 1046 D°
61	..	..	..	..	..
60	..	1	..	..	..
59	43(7)	54(14)	59(17)	48(16)	42(15)[2])
58	56[3])	45(1)	41(2)	52(2)	57
57	1	..	..	..	1
n	100(7)	100(15)	100(19)	100(18)	100(15)
A	**58.42**	**58.56**	**58.59**	**58.48**	**58.41**
σ	±0.518	±0.521	±0.497	±0.504	±0.516
P. E. A.	±0.0348	±0.0351	±0.0335	±0.0339	±0.0348
P. F. A.	±0.17	±0.18	±0.17	±0.17	±0.17
No. of D-rays					
16	..	..	..	..	1
15	41	20	36	34	52
14	55	66	62	65	47
13	4	14	2	1	
n	100	100	100	100	100
A	**14.37**	**14.06**	**14.34**	**14.33**	**14.54**
σ	±0.557	±0.584	±0.518	±0.505	±0.523
P. E. A.	±0.0375	±0.0393	±0.0349	±0.0340	±0.0352
P. F. A.	±0.19	±0.20	±0.17	±0.17	±0.18
No. of A-rays					
14	..	..	1	1	..
13	41	46	51	42	53
12	58	54	48	54	47
11	1	..	..	3	..
10	..	..	..	..	..
n	100	100	100	100	100
A	**12.40**	**12.46**	**12.53**	**12.41**	**12.53**
σ	±0.514	±0.504	±0.524	±0.573	±0.504
P. E. A.	±0.0346	±0.0339	±0.0352	±0.0386	±0.0339
P. F. A.	±0.17	±0.17	±0.18	±0.19	±0.17
No. of P-rays					
14	9	..	2	1	19
13	89	72	113	85	76
12	2	28	25	14	5
n	100	100	140[4])	100	100
A	**13.07**	**12.72**	**12.84**	**12.87**	**13.14**[5])
σ	±0.326	±0.451	±0.409	±0.368	±0.472
P. E. A.	±0.0220	±0.0304	±0.0233	±0.0248	±0.0318
P. F. A.	±0.11	±0.15	±0.12	±0.12	±0.16

[1]) Preserved at 1046 D°. [2]) + 1 with 19th and 20th vertebrae fused. [3]) 1 with 51st and 52nd vertebrae fused.
[4]) Larger sampel than usual employed. [5]) Left pectoral: A_{100} = 13.10.

Table 3. Series C. 9° (a -c: 9° → 6°). **H × G** 1943.

No. of vert.	Co. C No. 18	a: 191 D° No. 17 → 21	b: 299 D° No. 16 → 20	c: 425 D° No. 16 → 20	Co. C. No. 18 9° p. 999 D°	9° → 3° No. 18 → 2 432 D°
61	..	..	..	..	1	..
60	11(5)	6(1)	7(3)	4(4)	3(1)	5(3)
59	60(9)	60(11)	69(6)	74(5)	70(8)	64(6)
58	29	34(1[1])	24	22	26	31
57	..	..	..	..	..	..
n	100(14)	100(13)	100(9)	100(9)	100(9)	100(9)
A	**58.82**	**58.72**	**58.83**	**58.82**	**58.79**	**58.74**
σ	±0.610	±0.573	±0.533	±0.480	±0.529	±0.545
P. E. A.	±0.0411	±0.0386	±0.0359	±0.0324	±0.0356	±0.0367
P. F. A.	±0.21	±0.19	±0.18	±0.16	±0.18	±0.18
No. of D-rays						
16	4	3	6	6	7	2
15	85	72	71	70	81	60
14	11	25	23	24	12	37
13	..	..	..	..	..	1
n	100	100	100	100	100	100
A	**14.93**	**14.78**	**14.83**	**14.82**	**14.95**	**14.63**
σ	±0.383	±0.485	±0.514	±0.521	±0.438	±0.545
P. E. A.	±0.0258	±0.0326	±0.0346	±0.0351	±0.0294	±0.0362
P. F. A.	±0.13	±0.16	±0.17	±0.18	±0.15	±0.18
No. of A-rays						
14	..	..	..	..	..	..
13	26	42	31	27	25	17
12	73	56	66	72	71	67
11	1	2	3	1	4	16
10	..	..	..	..	..	..
n	100	100	100	100	100	100
A	**12.25**	**12.40**	**12.28**	**12.26**	**12.21**	**12.01**
σ	±0.459	±0.532	±0.515	±0.465	±0.496	±0.577
P. E. A.	±0.0310	±0.0359	±0.0347	±0.0313	±0.0336	±0.0389
P. F. A.	±0.15	±0.18	±0.17	±0.16	±0.17	±0.19
No. of P-rays						
14	21	28	22	14	40	
13	79	72	78	85	60	80
12	..	..	..	1	..	20
n	100	100	100	100	100	100
A	**13.21**	**13.28**	**13.22**	**13.13**	**13.40**	**12.80**
σ	±0.410	±0.452	±0.417	±0.368	±0.494	±0.403
P. E. A.	±0.0276	±0.0304	±0.0281	±0.0248	±0.0331	±0.0272
P. F. A.	±0.14	±0.15	±0.14	±0.12	±0.17	±0.14

[1]) This specimen has both 53rd + 54th and 51st + 52nd vertebrae fused.

Table 4. Series D. 6° (a—c: 6° → 9°). **H × G** 1943.

No. of vert.	Co. D No. 24	a: 155 D° No. 23 → 15	b: 242 D° No. 22 → 14	c: 442 D° No. 22 → 16	a: 155 D' No. 23 → 15
61	..	..	..	..	..
60	..	..	2(1)	1(1)	..
59	55(14)	27(12)	46(8)	48(7)	22(7)
58	45	73(1)	52(1)	51	77(4)
57	..	..	..	..	1
n	100(14)	100(13)	100(10)	100(8)	100(11)
A	**58.55**	**58.27**	**58.50**	**58.50**	**58.21**
σ	±0.503	±0.448	±0.545	±0.525	±0.435
P. E. A.	±0.0338	±0.0302	±0.0367	±0.0354	±0.0292
P. F. A.	±0.17	±0.15	±0.18	±0.18	±0.15
No. of D-rays					
16	2	3	..	1	..
15	62	65	45	65	68
14	36	30	50	34	32
13	..	2	5	..	..
n	100	100	100	100	100
A	**14.66**	**14.69**	**14.40**	**14.67**	**14.68**
σ	±0.518	±0.565	±0.588	±0.495	±0.471
P. E. A.	±0.0349	±0.0380	±0.0396	±0.0333	±0.0318
P. F. A.	±0.17	±0.19	±0.20	±0.17	±0.16
No. of A-rays					
14	2	..	..	1	..
13	53	27	23	55	35
12	44	67	69	44	57
11	1	6	7	..	8
10	..	..	1	..	..
n	100	100	100	100	100
A	**12.56**	**12.21**	**12.14**	**12.57**	**12.27**
σ	±0.559	±0.537	±0.570	±0.520	±0.602
P. E. A.	±0.0377	±0.0362	±0.0384	±0.0350	±0.0405
P. F. A.	±0.19	±0.18	±0.19	±0.18	±0.20
No. of P-rays					
14	14	21	11	15	18
13	85	79	87	84	82
12	1	..	2	1	..
n	100	100	100	100	100
A	**13.13**	**13.21**	**13.09**	**13.14**	**13.18**
σ	±0.368	±0.410	±0.351	±0.377	±0.387
P. E. A.	±0.0248	±0.0276	±0.0236	±0.0254	±0.0260
P. F. A.	±0.12	±0.14	±0.12	±0.13	±0.13

Table 5. E × F 1943 (♀ 58 + ♂ 59 vert.).

No. of vert.	3° A No. 6	6° B No. 12	6° D No. 19	9° C No. 13	3° → 9° No. 6 → 13 279 D°
61	3(1)	..	..	6(3)	1(1)
60	45(8)	25(9)	25(8)	61(12)	50(15)
59	50(3)	65(3)	67(4)	30(1)	48(8)
58	2	10(1)	8	3	1
n	100(12)	100(13)	100(12)	100(16)	100(24)
A	**59.49**	**59.15**	**59.17**	**59.70**	**59.51**
σ	±0.598	±0.576	±0.551	±0.629	±0.545
P. E. A.	±0.0403	±0.0388	±0.0372	±0.0424	±0.0366
P. F. A.	±0.20	±0.19	±0.19	±0.21	±0.18
No. of D-rays					
16	..	6	7	18	1
15	18	63	66	72	46
14	67	30	27	10	47
13	15	1	..	..	6
n	100	100	100	100	100
A	**14.03**	**14.74**	**14.80**	**15.08**	**14.42**
σ	±0.577	±0.581	±0.550	±0.526	±0.624
P. E. A.	±0.0388	±0.0392	±0.0371	±0.0354	±0.0420
P. F. A.	±0.19	±0.20	±0.19	±0.18	±0.21
No. of A-rays					
14	..	..	..	..	1
13	14	19	15	5	27
12	60	72	66	61	58
11	24	9	15	30	14
10	2	..	4	4	..
n	100	100	100	100	100
A	**11.86**	**12.10**	**11.92**	**11.67**	**12.15**
σ	±0.669	±0.532	±0.677	±0.639	±0.659
P. E. A.	±0.0450	±0.0358	±0.0456	±0.0430	±0.0443
P. F. A.	±0.23	±0.18	±0.23	±0.21	±0.22
No. of P-rays					
14	1	13	14	36	6
13	62	84	85	64	81
12	37	3	1	..	13
n	100	100	100	100	100
A	**12.64**	**13.10**	**13.13**	**13.36**	**12.93**
σ	±0.504	±0.389	±0.368	±0.484	±0.433
P. E. A.	±0.0339	±0.0262	±0.0248	±0.0326	±0.0292
P. F. A.	±0.17	±0.13	±0.12	±0.16	±0.15

Table 6. **A × C** 1942 (♀ 58 × ♂ 59 vert.). **B × D** 1942 (♀ 58 × ♂ 58 vert.).

No. of Vert.	A × C 4°	A × C 6°	A × C 8°	B × D 4°	B × D 6°	B × D 8°
61	..	..	..	4(1)	..	..
60	11(3)	9(2)	13(2)	104(23)	64(7)	96(10)
59	25(2)	40(1)	36	165(4)	220(1)	197(1)
58	1	1	1	6	16	7
57	..	..	..	..	..	..
n	37(5)	50(3)	50(2)	279(28)	300(8)	300(11)
A	**59.27**	**59.16**	**59.24**	**59.38**	**59.16**	**59.30**
σ	±0.510	±0.423	±0.478	±0.557	±0.492	±0.504
P. E. A.	±0.0565	±0.0403	±0.0455	±0.0224	±0.0192	±0.0196
P. F. A.	±0.28	±0.20	±0.23	±0.11	±0.10	±0.10

Explanation to the tables:

Co. = Control.
142 D° etc. = Number of day-degrees at which the batch of eggs or larvae has been transferred to another temperature.
No. 24, No. 22 → 14 etc. = Number of hatching-chamber in which the batch of eggs has been kept during the whole period or part of the period.
( ) = Number of pre-urostyle synostoses.
A, B, H and E: female Trouts.
C, D, G and F: male Trouts.
♀ 58 = female with 58 vertebrae.
a = first part of the incubation period until the eyed-egg stage.
b = period between eyed-egg stage and hatching.
c = period from hatching to about 500 day-degrees.
p = preserved.

Formulae employed: $\sigma = \pm \sqrt{\frac{\Sigma p a^2}{n-1} - b^2}$; $P.E.A. = \pm \frac{\sigma}{\sqrt{n}} \cdot 0{,}6745$; $P.F.A. = \pm \frac{\sigma}{\sqrt{n}} \cdot 0{,}6745 \cdot 5$.

Dansk Resumé.

Indledning.

Gennem den sidste Menneskealder er der indenfor Fiskeriundersøgelserne i alle Lande ofret særdeles meget Arbejde og store Midler paa Undersøgelser over Racekarakterer hos de økonomisk vigtige Fiskearter, idet man herved haabede at naa frem til et dybere Kendskab til Fiskebestandenes Lokalisering, Vandringer m. m. Særlig er Racekarakterer som Antallet af Hvirvler, Skæl og Finnestraaler anvendt i disse Undersøgelser, der paa mange Felter har bidraget til, at Kendskabet til de undersøgte Fiskearters Livshistorie er blevet meget udvidet. Naar man imidlertid ser paa de store Midler, der aarligt er anvendt paa disse Studier, er de opnaaede Resultater med Hensyn til Kendskab til Lokalisering, Vandringer o. l. hos vore Nyttefisk ikke imponerende. Og det er tilsyneladende ejendommeligt, at man ikke i højere Grad, end Tilfældet har været, ved Hjælp af Eksperimenter har søgt at faa mere indgaaende Kendskab til saa vigtige Forhold som de omtalte Racekarakterers milieubestemte Variation og deres Udviklingsmaade under forskellige ydre Kaar — for at se, hvor velegnede Karaktererne var som Middel til at fremme Kendskabet til Fiskebestandenes Lokalisering, Vandringer o. l.

Imidlertid ligger Aarsagen hertil lige for, idet det hidtil har været umuligt at opdrætte Saltvandsfisks pelagiske Yngel under eksperimentelle Forhold. Man har som bekendt hidtil ikke været i Stand til bl. a. at skaffe den helt spæde Yngel det passende Foder i tilstrækkelig Mængde, netop naar den skal begynde at æde. Efter at det lige før Krigens Begyndelse er lykkedes den norske Fiskeribiolog Gunnar Rollefsen at finde et velegnet Foder, nemlig de tidlige Stadier af Saltlagunekrebsdyret *Artemia salina*, vil der nu ogsaa være Muligheder for at eksperimentere med nogle af vore almindelige Saltvandsfisk, og mange Fremskridt vil derfor i nærmere Fremtid kunne opnaas paa de eksperimentelle Raceundersøgelsers Omraade.

Kun faa saadanne Eksperimenter er hidtil udført, dels med Laksefisk, dels med den levendefødende Aalekvabbe (*Zoarces viviparus*) og den tropiske, ligeledes levendefødende Tandkarpe *Lebistes reticulatus*. Det er hovedsagelig afdøde Professor Johs. Schmidt, der har udført disse Eksperimenter; men desuden bør nævnes C. McC. Mottley og endvidere Gunnar Rollefsen, hvis Forsøg imidlertid blev afbrudt ved Besættelsen af Norge i 1940, og derfor endnu ikke har givet os de Resultater, som vi har Lov at vente af dem.

Dette Forskningsomraade er altsaa meget lidt opdyrket.

Ved Oprettelsen af en særlig videnskabelig Afdeling i »Danmarks Akvarium« 1938 i nær Forbindelse med Fiskeri- og Havundersøgelsernes Laboratorier paa Charlottenlund Slot aabnedes der Mulighed for at paabegynde forskellige eksperimentelle Undersøgelser af Betydning for Fiskeriundersøgelsernes Arbejde. Saa snart Afdelingen var tilgængelig i Efteraaret

1940, paabegyndte jeg derfor en Række Forsøg med Henblik paa et nærmere Studium af de ydre Kaars Indflydelse bl. a. paa de meristiske Karakterer hos Fisk. Det var naturligt at anvende Havørreden, der havde vist sig at være et velegnet Objekt for Johs. Schmidt's Forsøg paa Carlsberglaboratoriet. Saltvandsfisk har endnu ikke kunnet inddrages i Undersøgelsen, da *Artemia*-Æg ikke kan skaffes i tilstrækkelig Mængde nu under Krigen. Forskellige Forhold medførte imidlertid, at de tekniske Installationer først efter et Par Sæsoner naaede frem til at virke nogenlunde tilfredsstillende, og de i dette lille Arbejde fremlagte Resultater er da ogsaa særlig opnaaet i Aarene 1942—43; Forsøgene maa dog kun betragtes som Indledningen til en Række fortsatte Undersøgelser over de ydre Kaars Paavirkning af forskellige Karakterer hos Fisk, og utvivlsomt vil det blive nødvendigt i de kommende Aar at revidere de Synspunkter, som hidtil er opnaaet, idet der overhovedet, som sagt, foreligger meget faa Undersøgelser paa dette Omraade.

Forsøgsanordning og Materialets Behandling.

I den videnskabelige Forsøgsafdeling i »Danmarks Akvarium« er der indrettet et lille Klækkeanlæg for Ferskvandsfisk, i hvilket Ørredæg som nævnt har været anvendt i en Række Forsøg siden 1940. Dette Anlæg er opbygget af Eternit og Cement; til Isolation er anvendt Korkplader. Anlægget er delt i 4 Afdelinger, hver med 7 Kamre, hvoraf det første er et Blandingskammer, hvori koldt og varmt Vand blandes, saaledes at man opnaar en Temperatur lidt under den ønskede; Finreguleringen af Temperaturen opnaas ved Hjælp af en Termoregulator og et Varmelegeme. Fra Blandingskammeret strømmer Vandet gennem de følgende 6 Kamre, hvori der er anbragt Celluloidkasser, i hvilke Ørredæggene klækkes. Vandstrømmen stiger op gennem Celluloidkassernes perforerede Bund, saaledes at Æggene eller Ynglen stadig faar tilført friskt Vand. Vandmassen i hele Anlægget fornyes 1—$2^1/_2$ Gange i Løbet af en Time. Der kan arbejdes med fire forskellige Temperaturer. I de Forsøg, der særlig omtales i det følgende, har der været anvendt de tre Temperaturer: 3°, 6° og 9°. Se Figurerne 1—2.

I nogle af de udførte Forsøg har det været af grundlæggende Betydning at foretage Omflytninger af Æg i forskellige Udviklingsstadier, saaledes at Æggene i et bestemt Stadium er blevet flyttet fra en Temperatur til en anden. For at fastlægge Tidspunkterne for Omflytningerne har jeg af praktiske Grunde anvendt Antallet af Daggrader (D°) regnet fra Befrugtningsøjeblikket. Som biologisk 0-Punkt er der regnet med 0° C; da kun Temperaturer mellem 3° og 9° er anvendt, vil der til samme Daggrad-Antal ret nøje svare samme Udviklingsstadium. Udvendig synligt Pigment i Embryonets Øje opnaas ved ca. 200 D°; Klækning finder Sted ved ca. 400 D°. Se Figur 3.

Til Belysning af Spørgsmaal vedrørende Temperaturens Indflydelse paa visse meristiske Karakterer som Hvirvelantal og Finnestraaleantal, er især Resultaterne anvendt fra et enkelt Par Havørred, ♀ H × ♂ G; desuden Resultater fra Yngel af nogle andre Ørreder (ialt 4 forskellige Par). Ørrederne har været Vildfisk; dog er Hannen G anvendt flere Aar i Træk, idet den hvert Aar er blevet moden i Akvariet.

De ydre Forhold for Æggene i de fire Afdelinger af Klækkeapparatet er saa vidt muligt søgt holdt ganske ens paanær med Hensyn til Temperaturen.

Da Dødeligheden i den vigtigste Serie (H × G) har været minimal, maa man gaa ud fra, at Forholdene i det store og Hele har været heldige for Æggenes Udvikling. Saaledes døde

af 7.400 Æg kun 30, eller 0.4 %; af de klækkede Unger døde kun ca. 2.4 %, skønt de blev holdt i Live uden Fodring, indtil hele Blommemassen var opbrugt; Yngelen konserveredes først ved ca. 800 D°; Trangen til Føde opstaar dog allerede ved ca. 600 D°.

Temperaturen har været holdt nogenlunde konstant ved 3°, 6° og 9°; oftest har Svingningerne i Døgnets Løb kun andraget højest 0.3°, men ved visse Uheld i Anlægget har den nu og da varieret indtil 1°, og i et Par Tilfælde indtil ca. 2° eller lidt mere. Se Figur 4. Da Forsøget f. Eks. ved 3° var udstrakt over ikke mindre end ca. 9 Maaneder (17. Dec. til 10. Sept.) har Uheld i Maskineri, Vandtilførsel o. l. ikke helt kunnet undgaas, men Uheldene maa dog antages ikke at have været af større Betydning for Hovedresultaterne af de nærværende Forsøg.

Vandets Iltindhold, der nu og da er analyseret, har oftest været over den Størrelse, som regnes for god i Ørredklækkerier, nemlig næsten stedse over 6.5 cm³ pr. Liter (med 5.6 og 8.4 cm³ som Ydergrænser). Ved de herskende Temperaturer har Iltprocenten været mellem ca. 71 og ca. 92 %, alleroftest over ca. 80 %. Hvorvidt Vekslinger i Vandets Iltmængde har nogen Indflydelse paa Antallet af Hvirvler eller Finnestraaler, ved man dog endnu intet om. Surhedsgraden, pH, har stedse været over 8, oftest omkring 8.2—8.3. Da Vandmasserne i de fire forskellige Serier har samme Oprindelse, har Vandets forskellige Indholdsstoffer, f. Eks. Nitrat og Fosfat, i Hovedsagen været ens i alle Serierne. Kun under Rensning af Klækkekasserne, Eftersyn o. l. har Lys haft Adgang til Æggene og Yngelen, der iøvrigt har været holdt i Mørke.

Yngelen er i Almindelighed konserveret, naar den var ca. 800 D° gammel, paa hvilket Tidspunkt Hvirvler og Finnestraaler er klart og tydeligt uddannet og Blommesækken helt eller næsten helt opbrugt. Man opnaar herved at faa et ret ensartet Materiale at arbejde med, idet Yngel, der er dræbt i dette Stadium, er ret ens med Hensyn til Skelettets Forbening, enten den har levet i 3° eller 6° eller 9°. Yngelen er konserveret i Formalin og farvet med Alizarin ifølge en ret omstændelig Metode; da Pigmentet affarves med Brintoverilte, vil alle Forbeninger i den lille Fisk fremtræde meget klart og tydeligt, naar den er klaret i Glycerin. Tælling af 100 Individer fra hver Prøve er foretaget under Mikroskop. Den sidste Straale i Ryg- og Gatfinne er dobbelt, men er talt som een. To sammenvoksede Hvirvler omkring 5.sidste Hvirvelelement (præ-urostyle Hvirvelsammenvoksninger) er talt som to hele Hvirvler; Antallet af saadanne Sammenvoksninger er angivet i Tabellerne 1—6, hvor Detailler af Tællingerne og de sædvanlig anvendte statistiske Angivelser vil være at finde. Ialt har 3350 Stykker Yngel været anvendt til Hvirveltællinger, de fleste ogsaa til Tælling af Finnestraaler.

Høje og lave Temperaturers Indflydelse paa det gennemsnitlige Antal Hvirvler og Finnestraaler hos Havørred.

Johs. Schmidt (1921 p. 21—23) har paavist, at Ørredæg af samme Forældrepar, der klækkes ved forskellige Temperaturer, giver Yngel, hvis gennemsnitlige Hvirveltal ikke blot er forskellige, men ved de anvendte Temperaturer er forskellige paa den ejendommelige Maade, at Prøver af Yngel klækket ved lave og høje Temperaturer (ca. 2° og 10°) begge har højere Gennemsnitsværdier end den Yngel, der klækkes ved intermediære Temperaturer, omkring 6—7°.

Disse Forsøgsresultater var ikke overensstemmende med de almindeligt fundne Værdier af Hvirveltal i Naturen, der oftest viser lave Værdier ved høje Temperaturer, høje Værdier ved lave Temperaturer. Og forskellige Forskere har derfor søgt at fortolke disse Resultater, men uden at naa til et almindeligt anerkendt Resultat (Kyle 1926, Johnsen 1936). Da det var nødvendigt for mine videre Forsøg at verificere Schmidt's Resultater, blev Forsøgene gentaget i Aarene 1941—43, og jeg kan fuldtud bekræfte dem (se Figur 5). I Naturen er et lignende Forhold ikke paavist, sandsynligvis fordi Ørreden overhovedet ikke vil eller kan gyde ved de højere Temperaturer, hvorunder dens Æg imidlertid eksperimentelt kan tvinges til at udvikle sig.

Det har saaledes været muligt at bekræfte Schmidt's Resultater med Hensyn til Hvirvelantallets Afhængighed af Temperaturen; man maa dog selvfølgelig tage det Forbehold, at det nævnte Afhængighedsforhold kun gælder under den givne Forsøgsanordning; Afhængigheden af Temperaturen for Antallet af Straaler i Ryg-, Gat- og Brystfinnen er derimod en ganske anden end Hvirvelantallets under den givne Forsøgsanordning.

Forsøgene med Yngel af Ørredparrene H × G og E × F er anvendt. Det maa først bemærkes, at disse Karakterer øjensynligt er lettere paavirkelige af Temperaturen end Hvirvelantallet, og endvidere, at en, selvom svag, Paavirkning synes at være mulig langt senere i Udviklingen; muligvis er dette dog betinget af Tidspunktet for Kalkaflejringen i disse Organer, idet Tælling af de mindste Finnestraaler kun er mulig, naar Kalkaflejring har fundet Sted; Finnestraalerne kan da først farves og altsaa tælles med Sikkerhed.

Resultaterne af Undersøgelserne er ret overensstemmende i de to Sæt af Ørreder, H × G og E × F, hvilket selvfølgelig tyder paa, at de er rigtige (se Fig. 6). For Rygfinnen er der en tydelig Stigning i det gennemsnitlige Antal Finnestraaler hos Prøver, der er klækket ved 3°, 6° og 9°; Stigningen andrager ca. 1 Finnestraale. Af Fig. 6 ser man endvidere, at Brystfinnen udviser omtrent samme Forhold som Rygfinnen, altsaa en Stigning i det gennemsnitlige Antal Straaler, parallelt med en Stigning i Temperaturen. Gatfinnen viser et mere uklart Forløb med Hensyn til det gennemsnitlige Antal Straaler, idet dette er lidet forskelligt ved de forskellige Temperaturer, men dog udviser et mindre Fald ved den højeste Temperatur (9°). Figur 6 og Tabellerne Side 52—56 viser de fundne Resultater.

Disse Karakterer synes ogsaa ifølge Erfaringer fra Naturen at være meget let paavirkelige af de ydre Forhold hos forskellige Benfisk; og det har i det store og Hele hidtil været vanskeligt at finde en almengyldig Lov for Variationen af Antallet af Straaler i Finnerne. Utvivlsomt maa man derfor gennem et stort og brydsomt eksperimentelt Arbejde, før man naar til en klar Forstaaelse af Finnestraaleantallets Afhængighed af Omverdensfaktorerne. I de nærværende Forsøg er Udslag udover ca. 1 Straale i Gennemsnit ikke opnaaet.

Tidspunktet for Fikseringen af nogle meristiske Karakterer hos Havørred.

Man har hidtil ikke været klar over, hvornaar i Udviklingen det endelige Antal Hvirvler er fikseret hos en Benfisk. Tidligere var man nærmest tilbøjelig til at anse Antallet af Hvirvler som udelukkende arveligt bestemt, hvorfor Antallet maatte være bestemt allerede ved Befrugtningen. Efterhaanden som Erfaringsmateriale viste, at nogen Ændring aabenbart er mulig som Svar paa visse Omverdensfaktorer, maatte man selvfølgelig forlægge Tidspunktet for Hvirvlernes Fiksering til et senere Stadium i Udviklingen, men hvor dette nogenlunde præcist var beliggende, har man ikke vidst. Udtalelserne herom er derfor ret

vage; KYLE har saaledes udtalt, at Tidspunktet maatte ligge saa sent i Udviklingen, at Chordaspidsen var bøjet opad, og Fiskelarven allerede var brudt ud af Ægget og svømmede rundt; andre har aabenbart tænkt sig Tidspunktet en Del tidligere. Alle Fiskearter forholder sig imidlertid ikke ens med Hensyn til Tidspunktet for Myomerudviklingen, Klækningstidspunktet i Relation til Myomerudviklingen o. l., hvorfor man sikkert staar overfor mange Undersøgelser, for de alment gyldige Regler for Hvirvlernes Fiksering kan uddrages. Jeg søger i dette Arbejde at paavise Forholdet hos Havorreden. Jeg har derfor undersøgt, om det er muligt hos Havorreden ad eksperimentel Vej at afgøre, paa hvilket Tidspunkt i Udviklingen det vil kunne lade sig gøre at paavirke Embryonet eller Larven paa en saadan Maade ved Ændring af Temperaturen, at Larven faar et andet Hvirveltal end det, som den vilde have faaet, hvis Udviklingen var blevet fortsat under den Temperatur, hvorunder den første Del af Udviklingen var begyndt. Desuden har jeg forsøgt at faa afgjort, hvor stort et Udslag i det gennemsnitlige Hvirvelantal det er muligt at frembringe eksperimentelt ved de anvendte Temperaturændringer. Andre Faktorers mulige Indflydelse beskæftiger os ikke i dette Arbejde.

Eksperimentet er den eneste Vej at gaa for at forsøge at afgrænse den Periode, i hvilken Fikseringen af det endelige, gennemsnitlige Hvirvelantal finder Sted hos Havorreden. Forsøgsserien H × G er anvendt hertil; og Princippet i Forsøgene har været at flytte nogle Hundrede Æg i forskellige Udviklingsstadier fra een Temperatur til en anden og derpaa undersøge, hvilket gennemsnitligt Hvirveltal Yngelen havde opnaaet, naar den var fuldt udviklet. De flyttede Prøvers Gennemsnitstal er saaledes sammenlignet med Tallene fra de Prøver, der som Kontrolprøver forblev ved samme Temperatur under hele Udviklingen. Der bygges altsaa i Hovedsagen videre paa det i foregaaende Kapitel fremhævede Forhold, at en intermediær Temperatur giver et lavt Hvirveltal, medens saavel de lave som høje giver højere Hvirveltal. Ifølge de spredte og usikre Udtalelser i Litteraturen troede jeg, at Perioden maatte ligge ret sent i Embryonaludviklingen, hvorfor jeg ved det første Aars Forsøg af Pladshensyn i Klækkeapparatet mente at kunne se bort fra de Stadier, da Embryonet endnu var meget ungt; det viste sig imidlertid, som det vil fremgaa af det følgende, at Perioden netop ligger i de meget tidlige Stadier.

I Forsøgene foretoges Omflytning mellem Temperaturerne 3°, 6° og 9° af Æg og Yngel i følgende Perioder: 1) kort før Pigmentdannelsen i Øjet begynder at vise sig, 2) i Tiden mellem »Øjenæg«-Stadiet og Klækningen og 3) kort Tid efter Klækningen af Larven, men betydeligt før Resorbtionen af Blommen begynder at vise sig. I hver Serie forblev mindst 500—600 Æg ved samme Temperatur under hele Udviklingen, altsaa som Kontrolprøver. Figur 8 og Tabellerne 1—5 giver iøvrigt alle Oplysninger om Omflytninger, Temperaturer, Tællinger o. s. v.

I Fig. 7 har jeg forsøgt rent teoretisk at vise, hvorledes Gennemsnitsværdierne fra en meget lang Række Omflytninger maa tænkes at være beliggende i Forhold til hinanden; eksperimentelt har det dog endnu kun været muligt at bestemme nogle faa Punkter paa denne teoretiske Kurve.

Det har vist sig, at Udviklingstiden fra Befrugtningen indtil det Tidspunkt, da Embryonet begynder at vise en vis Træghed mod Forandring af den til den paagældende Temperatur svarende numeriske Værdi, maa opfattes som en ganske indifferent Periode, i hvilken sandsynligvis de fleste af den paagældende meristiske Karakters Elementer anlægges. Den følgende Periode er derimod en Fikseringsperiode, i hvilken man maa antage, at de sidste Elementer anlægges og fæstnes; derefter synes en Milieupaavirkning praktisk taget at være udelukket.

Figurerne 8—13 viser Resultaterne, der er opnaaet ved Tælling af Hvirvlerne paa Yngelen fra de forskellige Prøver i Eksperimenterne; i Fig. 9—12 er der givet Frekvenspolygoner af Omflytningsprøverne og Kontrolprøverne fra hver Serie, og i Fig. 13 er der givet en Oversigt over Gennemsnittenes indbyrdes Beliggenhed i Koordinatsystemet.

Betragter vi nu Resultaterne fra alle de foretagne Omflytninger i Serierne A, B, C og D, vil man se, at i den lange Periode fra det Tidspunkt, da ca. 150 Daggrader er forløbet, indtil Yngelen er blevet klækket og er blevet indtil 800—1000 Daggrader gammel, har Hvirvelantallet ikke med fuld Sikkerhed kunnet ændres, hvilket altsaa vil sige, at Fikseringen af det endelige Hvirvelantal maa finde Sted paa et endnu tidligere Stadium i Udviklingen, nemlig betydeligt før »Ojenæg«-Stadiet er naaet.

Resultatet af en enkelt af Omflytningerne (den første i Serie D) kunde tyde paa, at Fikseringsperioden maaske ligger kort før eller ganske nær det Udviklingsstadium, der naas efter ca. 25—26 Dogn i 6° C. (ca. 150 D°), idet denne Prøve viser en iøjnefaldende Forskel fra alle de andre Prøver; Udslaget er ganske vist modsat rettet af det, man skulde vente, men dette kunde muligvis forklares derved, at Prøven maaske er flyttet nær en meget følsom Periode og derfor paa Grund af en Chockvirkning har reageret med det uventede Udslag.

En Betragtning af det Udviklingsstadium, som Embryonet befinder sig i efter et Forløb af ca. 150 Daggrader eller noget derunder, viser, at det paa dette Tidspunkt i Udviklingen endnu er meget ungt (se Fig. 3), men at Halespidsen dog er blevet fri af Æggeblommen; det er maaske i dette Stadium (eller i et endnu tidligere?), at de Cellemasser, hvoraf senere de bageste Hvirvler m. m. udformes, differentieres i Halespidsen.

Foruden de nævnte Omflytninger er der tillige foretaget Omflytning fra den laveste til den højeste Temperatur for at undersøge, om en saadan pludselig større Temperaturændring kunde have en udpræget Chockvirkning til Følge i et eller andet Udviklingsstadium. Forsøgsresultaterne (se Tabellerne Nr. 1, Nr. 3 og Nr. 5) udviser dog ingen Ændringer, naar Prøverne som i disse Tilfælde er flyttet efter ca. 200 Daggraders Forløb, hvilket saaledes ganske stemmer overens med de foran omtalte Forsøgsresultater.

Fortsatte Forsøg maa imidlertid udføres for at uddybe Kendskabet til disse Forhold, og de maa endvidere vise, hvorvidt en ganske svag Ændring i Hvirvelgennemsnittene (antagelig ikke over $^1/_5$—$^1/_{10}$ Hvirvel) kan opstaa efter ca. 150 Daggraders Forløb — nemlig ved Ændringer i Forbindelse med det 5.sidste Hvirvelelement i Rygsøjlen (de præ-urostyle Sammenvoksninger); se herom nedenfor Side 65.

Fikseringsperioden for de undersøgte Finners Straaleantal ligger senere end for Hvirvlerne, og dette maa anses for at være en naturlig Følge af Tidspunkterne for disse Karakterers Udformning i Løbet af Individets Udvikling. De udførte Forsøg synes at vise, at Antallet af Finnestraaler er mere ustabilt, lettere paavirkeligt end Hvirvelantallet, saaledes at en Udredelse af Forholdene vil blive en mere kompliceret Sag end for Hvirvlernes Vedkommende; der maa derfor i Fremtiden foretages talrige nye Forsøg for at klarlægge Sagen, idet de foreløbigt udførte Forsøg kun kan give en rent indledende Orientering, som dog giver Haab om, at man vil kunne naa vidt ad eksperimentel Vej.

I Figurerne Nr. 8 og 14—17 vil man finde en Oversigt dels over de foretagne Omflytninger, dels over Resultaterne. Og af Figur 3 kan man faa et rent orienterende Indtryk med Hensyn til Alderen af Embryonerne ved Udviklingen af de nævnte Finner. Man vil se, at Brystfinnerne kan skimtes anlagt allerede for ca. 150 D° er naaet, Gat- og Rygfinnerne først henimod 300 D°; men det maa hertil bemærkes, at Straalerne i Finnerne endnu ved Klækningen (alt-

saa ved ca. 400 D°) er meget langt fra at være udformet, saaledes at man kan tælle dem; i Ryg- og Gatfinnens midterste Del kan man begynde at skimte en Dannelse af Straalerne, naar Ungerne klækkes, men fortil og bagtil i Finnerne er Straalerne endnu ikke synlige; i Brystfinnen er Straalerne eller deres Basis endnu overhovedet ikke anlagt. Først langt senere i Udviklingen er Finnestraalerne udformet, saaledes at man kan tælle det endelige Antal. Det er derfor værd at bemærke, at der alligevel allerede meget tidligt i Udviklingen, endogsaa før »Øjenæg«-Stadiet er naaet, kan være en vis Træghed i Finnerne mod at ændre Straaleantallet fra de numeriske Værdier, som Kontrolprøverne faar.

Man kan, som det fremgaar af Kurverne, i visse Tilfælde faa helt uventede Udslag, som understreger, at ukontrollerede Faktorer har spillet ind. Ligeledes kan Udslagene være saa smaa, at der statistisk ikke er noget Bevis for en Ændring; dette gælder f. Eks. til Dels for Resultaterne vedrørende Ryg- og Brystfinne udviklet ved høje Temperaturer og for Gatfinne udviklet ved lave Temperaturer. Det er derfor muligt, at det kan være af en vis Betydning, hvorvidt den virksomme Temperatur under Udviklingen er højere eller lavere.

I en hel Række Tilfælde, i hvilke sikre Udslag er opnaaet, viser det sig, at en Ændring kan finde Sted over et længere Tidsrum, og Fikseringsperioden er altsaa ikke af nogen helt kort Varighed. De tre undersøgte Finner synes allerede meget tidligt at gaa ind i Fikseringsperioden. Brystfinnens Fikseringsperiode strækker sig øjensynligt fra det unge Øjenægstadium til en Tid efter Klækningen (til 1000 D° eller maaske endnu mere). For Ryg- og Gatfinnen synes den stærkeste Følsomhed for Paavirkning at ligge før Klækningen.

Og i Hovedsagen er Finnestraaleantallet fikseret betydeligt tidligere end i de Stadier, da man kan begynde at skimte Straalerne eller deres Basis, nemlig før Udklækningen.

Mellem Antallet af Straaler i Ryg- og Brystfinnen er der desuden iagttaget en iøjnefaldende positiv Korrelation (se Fig. 17).

Alle de foretagne Forsøg med Hensyn til Ændring af Finnestraaleantallets Paavirkelighed understreger dog som nævnt Nødvendigheden af langt mere omfattende Forsøg; en Betragtning af Resultater fra Fisk i Naturen viser tillige, at et omfattende Undersøgelsesarbejde er paakrævet for at udrede Forholdene her.

Anomalier i Hvirvelsøjlen og Betydningen af disse Dannelser.

I Hvirvelsøjlen hos Fisk kan der som hos andre Hvirveldyr optræde forskellige Slags Abnormiteter. Blandt disse indtager et Par Abnormiteter en ganske særlig Stilling; disse kendetegnes derved, at to (sjældent flere) af Hvirvelsøjlens Elementer, der er forkortede og sammensmeltede, stedse findes beliggende paa ganske bestemte Pladser i Hvirvelsøjlen, nemlig dels lige bag Hovedet, dels umiddelbart foran eller til Dels indbefattet i den bageste opadbøjede Del af Hvirvelsøjlen. I visse Tilfælde er den sidstnævnte Dannelse kun til at erkende derved, at der forekommer en Fordobling af den til Hvirvelelementet knyttede nedre, eventuelt ogsaa øvre Bue (se Fig. 18). Den første Slags Sammenvoksninger benævnes her post-craniale Hvirvel-Synostoser, den sidste Slags præ-urostyle Hvirvel-Synostoser (se Fig. 18). Medens den første Slags Sammenvoksninger ikke har nogen Betydning for vore nærværende Undersøgelser over Havørreden, fordi de aabenbart normalt er til Stede hos alle undersøgte Individer, kan den sidste Slags have nogen Betydning, idet Gennemsnittet af Hvirvelantallet kan paavirkes heraf, saafremt Sammenvoksningerne er til Stede i stort Antal. Hos visse Fisk,

som f. Eks. hos Rødspætter i Østersøen, kan Antallet af Individer med disse Sammenvoksninger endogsaa stige til næsten Halvdelen af alle Individer i en Prøve. Gennemsnitsantallet af Hvirvlerne kan altsaa paavirkes ret betydeligt af disse Dannelser, idet man kan være i Tvivl om, hvorvidt man skal tillægge dem Værdien 1 eller 2 Hvirvler. Schmidt (1921) har gjort det sandsynligt, at Værdien af de præ-urostyle Synostoser hos Ørreden i Virkeligheden er $1^1/_2$, og noget lignende synes ogsaa at gælde for disse Dannelser hos visse andre Fisk (f. Eks. hos Silden, ifølge Ford 1933).

En Bedømmelse af disse Dannelsers Betydning i Hvirvelsøjlen har ved Arbejdet med Havørreden vist sig at være nødvendig. I de forskellige Prøver af H × G-Helsøskende, der har levet under forskellige ydre Forhold, kan de forekomme hos 7 til 19 % af Individerne, i Gennemsnit hos 12.4 %; hos andre Ørredpars Yngel har endogsaa indtil 24 % været paavist. Det har derfor været nødvendigt at undersøge, om disse Dannelser kan frembringes eller paavirkes eksperimentelt. Selvom Spørgsmaalet endnu ikke er bragt til en endelig Afgørelse, synes det nærliggende at formode, at Dannelsen til Dels maa opfattes som en nødvendig Mekanisme eller Regulator for Organismen i de Tilfælde, hvor et højere eller lavere Hvirvelantal af en eller anden ydre Aarsag er blevet induceret under den embryonale Urhvirveldannelse og derpaa skal realiseres ved Hvirvellegemernes Forbening. Det bør bemærkes, at Hvirvlerne i denne Del af Rygsøjlen hos Ørreden og andre Fisk er de sidste, der forbener.

De hidtil foretagne Forsøg har vist, at Procentmængden af Sammenvoksninger har varieret i Antal fra eet Ørredpar til et andet, men hos tre af de fire anvendte Par fik den Yngel, der var udklækket ved den laveste Temperatur, de fleste Sammenvoksninger. Desuden viste Omflytninger af Ørredyngel fra en til en anden Temperatur, at en Forskydning af Procentmængden af Sammenvoksninger øjensynlig var mulig. Det synes altsaa muligt ved en Temperaturændring eksperimentelt at frembringe de ydre Tegn paa en typisk præ-urostyl Synostose; og denne maa derfor antagelig ligge skjult (latent) i det 5.sidste Hvirvelsegment i mange flere Tilfælde, end man erkender; dette støttes tillige deraf, at det nævnte Segment meget ofte er længere end baade det foranliggende og efterfølgende Segment, uden at man direkte tør tilskrive det Værdien af 2 Hvirvler.

Denne Mekanisme kan imidlertid, saavidt man endnu kan bedømme Forholdene, ikke gøres ansvarlig for hele den Ændring af det gennemsnitlige Hvirvelantal, som det har været muligt at frembringe i de nærværende Forsøgsserier, nemlig ca. $^1/_2$ Hvirvel.

Forsøgsresultaterne sammenlignet med visse saakaldte Raceforskelle hos nogle Saltvandsfisk samt afsluttende Bemærkninger.

Ved de foretagne Forsøg er det blevet vist, at en Forskel paa ca. 3° er nok til hos Ørreden at ændre det gennemsnitlige Hvirvelantal ca. $^1/_2$ Hvirvel. Dette er jo ikke nogen stor Forskel; men da man indenfor Fiskeriundersøgelserne har udskilt saakaldte Racer i Naturen ved Hjælp af lignende Forskelligheder i Hvirveltal, har jeg fremdraget et Par Eksempler fra Undersøgelser i Naturen til Belysning af Forholdene. Der er hertil anvendt Undersøgelsesresultater vedrørende et Par Saltvandsfisk, nemlig Silden og Rødspætten, hvis Hvirveltal er af en lignende Størrelsesorden som Ørredens, og hos hvilke Antallet af Hvirvelvarianter er noget lignende.

Et velegnet Sammenligningsmateriale foreligger af Sildeprøver fra Nordsøen (sammenstillet i Fig. 20 efter Schnakenbeck 1931). Prøverne underst og øverst til Højre i Fig. 20 opfattes som repræsenterende to Silderacer, nemlig Banksilden og Kanalsilden,

og de mellemliggende Prøver opfattes som sammensat af Blandinger af disse to Racer. Ved Siden af er opstillet Resultaterne af Hvirveltællinger af Prøver af Ørredunger, der er Helsøskende, men klækket ved forskellige Temperaturer. Man vil bemærke, at der praktisk taget ikke er nogensomhelst Forskel paa de to Rækker af Frekvenspolygoner; men der er den uhyre, vidtrækkende Forskel, at medens Sildeprøverne er blevet anset for at repræsentere to veladskilte Racer i Naturen, er Ørredprøverne altsaa alle Afkom af samme Forældrepar, men modificerede i Hvirvelantal af en Temperaturforskel, som Arten let vilde kunne finde i Naturen. Det er selvfølgelig ikke hermed bevist, at de to Grupper Sild ikke er genetisk forskellige; men det er indlysende, at Beviset herfor maa føres paa anden Maade end fortrinsvis ved Anvendelse af de benyttede smaa Forskelligheder i Hvirvelantal.

Foruden Prøven af Sild er det tillige illustrerende at betragte Figur 22, der viser Frekvenspolygoner af Rødspættens Hvirvelantal rundt om Island; man har her den samme gennemsnitlige Hvirvelforskel, som fandtes saavel hos Ørredprøverne som hos Sildeprøverne, nemlig ca. $^1/_2$ Hvirvel mellem de Prøver, der viser størst Forskel; modsat Schnakenbeck 1931 opfatter vi ogsaa denne Forskel som frembragt fortrinsvis af Temperaturforskelligheder i de Vandmasser, hvori Rødspætteægget gennemløber sin Udvikling (Forskellen er antagelig ca. 4°); og Eksemplet kan betragtes som et smukt Eksperiment udført af selve Naturen, idet Temperaturfaldet rundt om Island kan sammenlignes med det Temperaturfald, som man kunde tænke sig at etablere i en Serie Akvarier for eksperimentelt at undersøge Temperaturens Indflydelse paa Hvirveltallet.

De nævnte Eksempler synes klart at understrege, at man med Forsigtighed maa behandle saadanne Raceforskelligheder, som kun støttes af mindre Forskelligheder i meristiske Karakterer, og Eksemplerne fremhæver Berettigelsen af den Opfattelse, der i de seneste Aar har bredt sig blandt Fiskeribiologer, nemlig at de meristiske Karakterer hos hver enkelt Art eller geografisk Race er i Besiddelse af en vis, ikke helt ubetydelig Labilitet, hvorfor man med Mistillid maa betragte en ensidig Anvendelse af subtile Raceforskelligheder til Lokalisering af Fiskebestande, Undersøgelser af disses Vandringer o. l. Den eksperimentelle Raceforskning vil nu — da i hvert Fald nogle Saltvandsfisk (iflg. Rollefsen 1940) kan inddrages i Forsøgene — kunne blive et meget værdifuldt Instrument for Afgørelsen af, om Forskelligheder i meristiske Karakterer er af fænotypisk eller genotypisk Art; at mindre Forskelle i disse Karakterer ogsaa kan være genotypisk fæstnede er allerede for 25 Aar siden vist af Schmidt (1919, 1920).

Og der er ikke Tvivl om, at et fortsat Arbejde paa den eksperimentelle Raceforsknings Omraade vil blive af stigende Betydning for Fiskeribiologien, bl. a. fordi det er vigtigt at naa til en sikker Afgørelse af, i hvilket Stadium af de forskellige Nyttefisks Udvikling en Paavirkning er mulig af en saa stærkt benyttet Racekarakter som f. Eks. Hvirvelantallet, og desuden til en Afgørelse af, hvor store Udslag Paavirkningen kan udløse.

Det er dog endnu altfor tidligt at forsøge paa teoretisk at udrede, hvorledes de enkelte Milieufaktorer i Virkeligheden paavirker de meristiske Karakterer, idet vi faktisk endnu kun kender en ganske lille Smule til Temperaturens Indflydelse, og maaske knapt engang det, da Temperaturens Virkninger muligvis er regulerede af en eller flere andre Faktorer, som vi endnu ikke har Hold paa.

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